A Dental Topographic Analysis of Deciduous Tooth Wear in Hominoids

by

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ABSTRACT

Early weaning, slow somatic and dental growth, and late age at reproduction are all part of a suite of energetic trade-offs that have shaped human evolution. A similar suite of energetic trade-offs has shaped the evolution of the indriid-palaeopropithecid clade, though members of this clade exhibit extremely fast dental development and nearly vestigial deciduous teeth. The development and functional occlusion of the primary postcanine dentition (i.e., deciduous premolars and molars) coincides with several life history parameters in great apes and indriids. This dissertation explored great ape dental macrowear, molar development in indriids, and molar size in lemurs with a broader goal of improving reconstructions of life history profiles in extinct primates. To this aim, macrowear and dental development were analyzed in apes and lemurs, respectively. Occlusal casts (six great ape species; N=278) were scanned to track mandibular fourth deciduous premolar (dp_4) macrowear. Utilizing dental topographic analyses, changes in occlusal gradient and terrain were quantified. A subset of the great ape data (four species; n=199) was analyzed to test if differences in dp_4 wear correlate with age at weaning. Using dental histology, molar development was reconstructed for *Indri indri* (n=1) and *Avahi laniger* (n=1). Life history and molar size data were collected from the literature. The results of this dissertation demonstrate that most great apes exhibited evidence of topographic maintenance, suggesting dp_4s wear in a manner that maintain functional efficiency during growth and development; however, the manner in which maintenance is achieved (e.g., preservation of relief or complexity) is species specific. Dp_4 macrowear is not correlated with age at weaning in great apes and is probably unreliable to reconstruct

age at weaning in hominins. The pace of molar development in members of the indriid-palaeopropithecid clade did not correlate with body or brain size, an association present in several other primates. Associations of molar size with age at weaning suggest that expanding other developmental models (e.g., the inhibitory cascade) to life history is worth consideration. The broad variation in macrowear, dental development, and size highlights how the primary dentition may correlate with different life history parameters depending on the species and ecological setting, an important consideration when using teeth to reconstruct life history profiles.

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CHAPTER 1

INTRODUCTION

Outline

This dissertation is organized into three papers, with an introduction to review broader theoretical topics and a conclusion to summarize future research directions. The broader goal of this dissertation is to explore possible relationships among age at weaning, deciduous tooth wear, and dental development in primates. To this aim, this project first tests whether deciduous teeth, specifically the mandibular fourth deciduous premolars (dp_4s) in great apes, wear in a manner that maintains the dental topography. Second, this project tests whether differences in dp_4 wear in great apes can be attributed to age at weaning. Finally, this dissertation explores whether aspects of dental development correlate with life history variables among lemurs.

In 1991, Aiello et al. noted that in juvenile hominins with similar stages of dental development those attributed to *Australopithecus* had less wear when compared to juveniles attributed to *Paranthropus*. They noted a similar pattern in great apes—juvenile gorillas exhibited greater wear than the other great ape species. They hypothesized that the differences in wear might have been due to diet and/or age at weaning. Therefore, a large part of this dissertation focuses on testing whether age at weaning can be attributed to, at least partially, occlusal wear differences observed in great apes species (Chapter 3); however, it was first necessary to establish a baseline understanding of macrowear on dp_4 occlusal surfaces (Chapter 2). Occlusal wear was quantified using some of the most sophisticated techniques currently available (i.e., dental topographic analyses; reviewed

in Chapter 2). Finally, dental development and its application to reconstructing life history profiles of extinct lemur species are explored (Chapter 4).

Life History Theory and Weaning

The main premise of life history theory states that all organisms must balance energetic trade-offs for growth, maintenance, and reproduction (reviewed in Stearns, 1992; Roff, 2002). Many life history variables (e.g., gestation length, age at first reproduction, age at weaning) reflect how an organism balances these energetic trade-offs. A life history profile describes the sequence and timing of life history "stages" (i.e., infancy, juvenile period, adulthood) that an individual traverses to grow, develop, and reproduce (e.g., Metcalf and Pavard, 2007; Catlett et al., 2010). Since individual longitudinal data are difficult to obtain, life history profiles typically summarize the species' average length of time or age at key life history stages (e.g., average gestation length, average age at weaning). A more common term for life history profile is life history strategy. Some researchers prefer the phrase *life history profiles* as opposed to *life history strategies* because the word *strategy* connotes that organisms consciously plan life history events; therefore, this project uses the phrase *life history profile* (Dean and Leakey, 2004; Catlett et al., 2010; Schwartz, 2012; Zehr et al., 2014).

The timing and duration of life history events demarcate how animals allocate energetic costs throughout their lifespan; however, several additional factors need consideration. Organisms must negotiate energetic trade-offs to maximize fecundity while constrained by phylogeny, genetics, biomechanics, ecology, and physiology (Roff, 2002). A number of these constraints have been noted in the field of evolutionary

anthropology. For example, ecological factors, such as the harsh, but cyclical, modern environments in Madagascar help explain the synchronous weaning patterns observed in many lemurs (e.g., Wright, 1999; Ohba et al., 2016). Recently, researchers studying humans and callitrichids have documented how cooperative breeding promotes prosocial behaviors in childrearing practices, which, in turn, releases a mother from physiological constraints that allow her to reproduce more quickly (e.g., Burkart et al., 2009).

Compared to our closest living relatives, the great apes, modern humans wean their young at ages (~2-4 years) that are much earlier than expected for our body and brain sizes (reviewed in Chapter 3). Extensive studies on the evolution of primate and modern human behavior support the hypothesis that cooperative breeding in modern humans alleviates mortality risks that are associated with weaning altricial young but delaying age at first reproduction. (e.g., reviewed by Hrdy, 2009). Folded into the broader cooperative breeding hypothesis is also the grandmothering hypothesis, which helps explain why human females live long past their reproductive years (Williams, 1957; Hawkes et al., 1998). Women past their reproductive years can improve their fitness by assisting their daughters with childrearing, enabling younger women to wean their offspring early. Early weaning shortens interbirth intervals and younger women can produce offspring more frequently (Hawkes et al., 1998; Hawkes, 2006; Thompson, 2013). Other research also examines alloparenting roles by other members of a social group (e.g., fathers, siblings) (e.g., Kramer, 2011; Kramer and Russell, 2015). While the cooperative breeding hypothesis can account for *how* humans can raise energetically costly offspring with protracted growth (Isler and van Schaik, 2012), it does not solve the debate *when* early weaning evolved within the hominin lineage (e.g., Kelley and Schwartz, 2012; Schwartz,

2012; Smith, 2013).

When Dart (1925) announced the discovery of the Taung child (*Australopithecus africanus*), he noted that the deciduous dentition and first molar had fully erupted, a developmental status that corresponds to a six-year-old human child. Both Le Gros Clark and Dart thought that the level of dentine exposure in the deciduous dentition of the Taung child suggested a slower, human-like maturation schedule (Le Gros Clark, 1947; Dart, 1948). In 1975, Mann explored the evolution of human growth and development by complementing the previous research on tooth wear with detailed analyses of dental development. By comparing the extent of tooth and root formation in humans, chimpanzees, and the then available sample of South African hominin juveniles, he concluded that a slow, human-like growth and developmental schedule had an ancient origin and evolved early in the hominin lineage.

The limitation of Mann's (1975) work was that the aging categories were based on *relative* ages, as there was no way to establish the absolute age at death from a juvenile specimen. Following 1975, the field of dental histology advanced and provided a method to obtain the absolute age at death if a juvenile specimen had died before the completion of dental development (e.g., Bromage and Dean, 1985). As discussed in Chapter 4, when teeth develop they deposit hourly and periodic incremental lines (similar to trees). These dental microstructures provide a sort of 'calendar' that allow researchers to determine an absolute age at death for a juvenile specimen (e.g., reviewed by Schwartz and Dean, 2008).

Subsequent research applied these advanced dental histological techniques to the hominin fossil record, and, for first the time, researchers were able to obtain absolute

ages at death for juvenile hominins (e.g., Dean et al., 2001; Macchiarelli et al., 2006; Smith et al., 2007). Mann's conclusion proved to be an oversimplification, as early hominins seemed to have faster dental developmental schedules, and likely faster maturation schedules, more similar to chimpanzees rather than modern humans. The faster pace of dental development observed in early hominin fossils suggests that the protracted growth and developmental schedule in modern humans is a more recent phenomenon than Mann suggested (e.g., Smith et al., 2007).

As research progressed, paleoanthropologists realized that the categorization of growth and developmental schedules as either being fast (chimp-like) or slow (human-like) to describe hominin development obscured the tremendous amount of variation that existed (e.g., Smith et al., 1994; AlQahtani et al., 2014). While the molars in modern humans emerge at much later ages than the molars in apes, the ages at which the anterior dentition emerge greatly overlap. For example, the maxillary or mandibular M1 emerges at ~6 years of age in modern humans (e.g., Smith et al., 1994; AlQahtani et al., 2014) and ~3.5-4.0 years in chimpanzees (e.g., Zihlman et al., 2004). In contrast, the maxillary central incisors in humans emerge ~7.5-8.5 years of age (e.g., Smith et al., 1994; AlQahtani et al., 2014) and in a wild population of chimpanzees the maxillary central incisors are reported to emerge ~6.3-8.4 years of age (Zihlman et al., 2004). The emergence of the canines (even taking into account sex differences due to canine sexual dimorphism in great apes) also overlaps in humans (i.e., 10.5-12.5 years) and a wild population of chimpanzees (10.1-10.8 years of age, with a projected age range of 8.5 to 14.2 years). The absolutely faster pace of dental development between humans and chimpanzees is primarily concentrated on the posterior teeth (Dean and Wood, 1981).

Comparable data for absolute ages of incisor and canine emergence, with reliable ranges, are still lacking for wild gorillas and orangutans.

Aside from the absolute differences in the timing of molar emergence between humans and great apes, the timing of the mandibular first molar (M_1) emergence has especially sparked interest in paleoanthropology. In primates, Smith (1989, 1992) demonstrated strong statistical correlations between the emergence of the M_1 and age at weaning. Her work on the associations between dental development and life history variables complemented the dental developmental work on how the microstructures could be used to chart the absolute pace of dental development. If researchers could get exact ages at death and quantify the rate of dental development, then, perhaps, paleoanthropologists could use dental development to reconstruct the paleobiology of extinct hominins, ushering in an exciting era of new research for evolutionary anthropologists. In the decades following Smith's seminal work, researchers found that the associations between M_1 emergence and age weaning (among other life history variables) were less consistent in great apes (reviewed by Smith, 2013), and the precise relationship between dental development and life history variables to reconstruct hominin life history and are still being investigated (e.g., Kelley and Schwartz, 2012). Still, Smith's work provides an important null hypothesis (i.e., the emergence of M1 is the same as age at weaning) for testing associations between tooth emergence and life history.

Generally, weaning is considered stressful for juveniles. Weaning marks a transitional period when a juvenile must acquire foraging independence to be self-sustaining (Langer, 2008). Mothers must balance their own energetic needs to ensure their future reproductive fitness. Trivers (1974) hypothesized how the process of weaning

is an example of how mothers and their offspring have competing interests—mothers need to limit care to focus on future reproductive efforts and infants need to maximize care to ensure their future reproductive success. Within this context, it is predicted that the cessation of suckling is a stressful period in a juvenile's life as a reliable energy resource (i.e., mother's milk) is slowly, or abruptly, eliminated. As Trivers predicted, in species where the cessation of suckling is more abrupt, infants do experience signs of elevated stress (e.g., Mandalaywala et al., 2014).

In contrast, Bateson (1994) observed that many mother-infant conflicts were less hostile than Trivers (1974) predicted. Bateson (1994) hypothesized that behavioral outbursts from older (but not yet weaned) juveniles may reflect genuine needs and, based on the available behavioral data, mothers are much more willing to accommodate needy offspring than Trivers' (1974) model predicts. Although data are limited, while great ape juveniles experience some conflict shortly before being fully weaned, it is minimal in comparison to several other primates (Lathouwers and Elsacker, 2006). Part of the explanation as to why the mother-infant conflict is minimized in great apes is because great apes are non-seasonal breeders and lactate for several years. Van Noordwijk et al. (2013) explain that non-seasonal breeders can allow for greater flexibility in the timing of weaning for their offspring since seasonal breeders must be reproductively available for the next mating season. Non-seasonal breeders, like great apes, will be reproductively available after the dramatic reduction of suckling bouts (Lee, 1996). In this context, multiyear lactation is less costly for non-seasonal breeders, as the frequency of suckling seems to induce postnatal amenorrhea rather than lactation itself (Stewart, 1988; McNeilly et al., 1994; Vitzthum, 1994).

The introduction of supplementary foods influences the frequency and duration of suckling sessions (Howie et al., 1981). Therefore, the potential energetic and reproductive costs great ape mothers incur may be reduced if infants start to ingest supplemental foods relatively early (Hayssen, 1993). At least in chimpanzees, the first two years of life are the most energetically costly for lactating mothers (Thompson et al., 2012). Extended studies on one wild chimpanzee population found that lactating mothers with older juveniles can conceive (Smith et al., 2013). Therefore, milk used as a dietary supplementation for older juveniles may help reduce some of the energetic and reproductive costs incurred during prolonged lactation. In addition, for socially complex primates, like great apes, juveniles will also suckle to strengthen social bonds with their mothers, making it difficult for researchers to ascertain whether older juveniles are suckling to fulfill a nutritional need or are comfort-nursing (Bateson, 1994; Kennedy, 2005; Dirks et al., 2010; Reitsema, 2012). While weaning takes several years in all great apes, fully weaned juveniles still require several additional years to complete body growth and to reach age at first reproduction (e.g., Leigh, 1994; Robson et al., 2006).

Young juvenile primates usually initiate the weaning process when they begin to mouth or sample foods their mothers eat, but primate mothers usually complete the process of weaning when they actively prohibit juveniles from nursing (Langer, 2008). Therefore, selection should favor mothers to cease nursing when food resources are plentiful and a still growing juvenile primate, but now denied mother's milk, can attain enough nutrition from a resource-rich environment. Strict seasonal breeders seem to follow this pattern and, if resources are scarce, for example due to limited rainfall, the infant and juvenile mortality rates can be high (e.g., Janson and van Schaik, 1993;

Godfrey et al., 2004; King et al., 2005; Kappeler and Fichtel, 2012). Given the expectation that the post-weaning period is potentially costly to young primates, selection should favor certain developmental patterns, such as the emergence of M1 to coincide at weaning (i.e., a null hypothesis). The addition of the M1 to the deciduous postcanine dental battery would increase the chewing surface area to breakdown foods more effectively, thus mitigating some of these energetic costs (e.g., Smith, 1992; Janson and van Schaik, 1993; Godfrey et al., 2003; Mahoney, 2015).

Development of the Primary Postcanine Dentition

Several excellent textbooks are available that provide detailed descriptions of dental development (e.g., Nanci, 2003; Berkovitz et al., 2011); therefore, only the relevant highlights of dental development are summarized below.

Great apes develop two sets of teeth, commonly referred to as the deciduous (or milk) teeth and permanent (or adult) teeth. The primary dentition includes both the deciduous dentition and the molars. While the deciduous dentition is generally replaced, the molars are not replaced in primates; therefore, the molars, along with the deciduous premolars, constitute the primary postcanine dentition. In primates, all of the deciduous teeth and, minimally, the M1s initiate *in utero*.

In humans, at about ~6 weeks from conception two thickened bands of epithelium form at the sites of the future jawbones. This primary epithelium band segregates into the vestibular lamina and dental lamina. The vestibular lamina is the future site of the mouth, lips, and cheeks, and the dental lamina will contribute to the development of the teeth. After the formation of the dental placode, the future site of a tooth, each tooth germ will

develop through a series of three stages (i.e., bud, cap and bell). Throughout tooth formation, the dental lamina will continue to extend with future tooth organs budding off. Deciduous premolars and molars grow from the same extension of dental lamina. In primates, the molars are not replaced, as a primate only develops one set of molars; therefore, the molars are part of the primary dentition. The deciduous incisors, canines, and premolars are replaced, and the succedaneous teeth (i.e., permanent incisors, canines, and premolars) develop from the successional dental lamina. The succedaneous dentition then continues through the three main stages of development and develops like the primary teeth. During the last stage, the bell stage, the tooth acquires its final shape and histodifferentiation can begin. This process includes differentiation of ameloblasts and odontoblasts, the cells that form the enamel and dentine, respectively. As discussed in Chapter 4, these cells deposit the enamel and dentine matrix in ~24 hour cycles, leaving periodic lines that dental histologists can count to calculate how long it took for that tooth to grow, as well as provide an absolute age at death in extant and extinct juvenile specimens.

At least in the case of the primary postcanine dentition, the close communication of the tooth germs of the dental lamina results in an inhibitory cascade effect. The development of the anteriormost primary postcanine tooth regulates the ratio of activator and inhibitor molecules that affect the timing of initiation (i.e., when the tooth starts to develop) and the final size of the tooth crown of the subsequently developing posterior tooth (Kavanagh et al., 2007). As a result, this relationship has predictive power and can be used to estimate sizes of other postcanine primary teeth (Evans et al., 2016). This also implies that selection on deciduous premolars can influence both the crown size and

timing of initiation of subsequently developing molars. Thus, when the deciduous premolars are considered within a functional and developmental context it becomes apparent that selection acting on the deciduous premolars may affect the development and morphology of the molars (Evans et al., 2016), highlighting the evolutionary importance of these primary teeth.

Tooth Wear and Dental Ecology

A fundamental tenet of paleontology is that the occlusal surfaces of teeth are adapted to meet the functional demands of particular dietary regimes (e.g., Owen, 1840; Osborn, 1907; Simpson, 1936; Kay, 1975; Lucas et al., 1986; Teaford and Ungar, 2000; Ungar, 2010). The same dental features (e.g., hardness, morphology, enamel thickness, occlusal area) that allow teeth to effectively process particular diets are also the same qualities that enable teeth to counteract the irreversible effects of wear (Janis and Fortelius, 1988; Ungar and M'Kirera, 2003; Lucas, 2004). For example, the molars of predominately folivorous primates exhibit pronounced shearing crests (Kay, 1975), and research has demonstrated that primate molars adapted for highly folivorous diets tend to wear in a manner that maintains, or even increases, their shearing capacity, at least for a time (King et al., 2005; Glowacka et al., In Press). A wear-pattern that maintains shearing capacity is advantageous for primates that eat a tough, leafy diet because it enables the tooth to maintain functional efficiency throughout a large proportion of the animal's lifespan.

While the precise contribution of external agents, such as phytoliths or exogenous grit, to tooth wear remains debated (Baker et al., 1959; Sanson et al., 2007; Rabenold and

Pearson, 2011; Lucas et al., 2013; Galbany et al., 2014; Lucas et al., 2014), there are three recognized categories of wear: abrasion, attrition, and erosion (reviewed by Kaidonis et al., 2012). Abrasion occurs via mechanical forces from external agents. Tooth-to-tooth contact causes attrition, and erosion occurs via extrinsic and intrinsic chemical reactions with the teeth, such as acid erosion from food or gastric acids (El Aidi et al., 2008; Moimaz, et al., 2013). Generally, attrition and abrasion affect only the occlusal surfaces of teeth. Dental erosion can affect the entire tooth crown, even portions that do not occlude with other teeth or are directly involved in mastication, such as the tooth crown near the gum line. The effects of wear can be studied at both the macro and micro level. Microwear analyses measure how the microscopic texture changes on the occlusal surface, and extensive research has demonstrated microscopic surface changes on the occlusal surface provide an excellent indicator of the foods the animal recently ingested (e.g., Walker et al., 1978; Teaford, 1988; Scott et al., 2012). Since the focus of this research project is on macrowear, microwear will not be considered further.

Researchers focusing on either the clinical or evolutionary implications of the biomechanical processes of tooth wear have made great progress in parsing the mechanics of wear in both laboratory and computer simulation experiments (e.g., Chai et al., 2009; Lee et al., 2011; Constantino et al., 2012; Keown et al., 2012; Berthaume, et al., 2013; Kupczik and Lev-Tov, 2014). For many evolutionary anthropologists and primatologists, the study of tooth wear has several important ecological implications, driving the emergence of the field of dental ecology. Dental ecology studies the interaction of teeth and the environment in living animals (Cuozzo and Sauther, 2012; Evans, 2013). More specifically, dental ecology attempts to focus on how teeth alter due

to intrinsic and extrinsic environmental selective pressures, which contrasts with other biological roles of teeth (e.g., as reflected in the canine honing complex discussed below).

Many dental ecology studies track tooth wear in different age groups or niches. For example, recent work on a wild population of ring-tailed lemurs (*Lemur catta*) linked tooth-wear patterns with the force loads required to crack the casings of tamarinds, which produced a particular feeding behavior (i.e., multiple biting episodes on the postcanine teeth inducing micro-cracking in the enamel) (Yamashita et al., 2012). The more strict definition of dental ecology focuses on extant species; however, studies conducted within a dental ecology theoretical framework allow researchers to develop models and methodologies using extant species to reconstruct diets and palaeoenvironments (e.g., Godfrey et al, 2012). For example, isotopic analyses tracking dietary changes in different spatial and temporal populations provide important insight into habitat and environmental variation of extant and extinct species, including hominins (e.g., Smith et al., 2010; Cerling et al., 2013; Carlson and Kingston, 2014; Sponheimer et al., 2013; Schoeninger, 2014).

While the principal function of teeth is to assist in digestion, primate teeth can assume several other biological roles that are not directly related to diet. A primary example is the canine. Several species of primates (e.g., gorillas, orangutans, baboons) exhibit both body size and canine size sexual dimorphism. In this group of primates, males have larger canines than females to engage in male-to-male combat and gain access to females. Given the important social role of canines, intraspecific canine size comparisons enable paleoanthropologists to reconstruct aspects of mate competition from fossil specimens (e.g., Plavcan, 2001; Plavcan, 2003). However, most research on the

primate dentition within a dental ecology framework focuses on the permanent dentition, with limited attention given to the non-human primate deciduous dentition (but see Ashton and Zuckerman 1952; Trotter et al. 1977; Aiello et al. 1991; Swindler 2002; Ankel-Simons 2007; Elgart 2010; Ingicco et al. 2012; Hardin and Legge 2013).

The reduced size of the deciduous dentition, relative to the permanent teeth, allows smaller, but growing, jaws to maintain proper occlusion (e.g., Baume, 1950), and improper maintenance of deciduous teeth or premature exfoliation may affect proper dental development (e.g., Macena et al., 2011; Nanci, 2013). Masticatory forces induced via chewing (or teething) also play an important role in generating proper craniofacial development, as it affects bone growth (e.g., Kiliaridis, 2006; Tanaka and Sato, 2008). Schwartz (2012) reports that in modern humans the timing of postcanine tooth emergence, including the deciduous premolars, coincides with cranial growth in a manner that maintains biomechanical optima relative to the temporomandibular joint, masticatory musculature, and occlusal bite points. These results suggest that strong selective pressures constrain the timing of primary postcanine dental emergence with craniofacial development.

In comparison to the succedaneous dentition, primary teeth develop faster, as they must attain functional occlusion within a shorter timeframe (e.g., Macchiarelli et al., 2006, Birch and Dean, 2009; Mahoney, 2015). In primates, a large proportion of the deciduous dentition (e.g., complete crowns) is fully developed at birth (Smith et al., 1994; Swindler, 2002), and in some strepsirrhine primates, extensive M1 and even M2 development is observed (Schwartz et al., 2002; Godfrey et al., 2006; Catlett et al., 2010; Chapter 4). However, the functional contribution of deciduous teeth appears to vary among primate

species. In primates with extremely fast dental development (e.g., indriids), the deciduous teeth shed very quickly and, in some primates, such as tarsiers, the deciduous teeth shed *in utero* and can even be considered vestigial (Smith et al. 1994; Godfrey et al. 2005a; Chapter 3). Metabolic factors can vary the rate of dental development, such as when smaller-bodied mouse lemurs undergo seasonal torpor (Blanco and Godfrey, 2013). In contrast to lemurs, species with much longer dental developmental schedules, such as the great apes, the deciduous dentition is retained for several years and remains in functional occlusion both before and after the multiyear weaning process (Dean and Wood 1981; Aiello et al. 1991; Smith et al. 1994; see Figure 3.1 in Chapter 3). The wide variation in primate deciduous tooth development and shedding schedules suggests that deciduous teeth may be involved in different biological functions depending on the primate species and ecological settings.

Conclusion

Given the developmental linkage between molars and deciduous premolars, understanding how selection may have acted on dp_4 macrowear could reveal two untapped avenues of research. First, studying dp_4 wear patterns may elucidate how juveniles use their teeth to forage effectively, and thus minimize their mortality risks. Second, selection acting on dp_4s may affect the morphology of the molars, a tooth type that must function for decades in long-lived primates and is correlated with many life history variables.

In Chapter 2, "Dental topographic analyses of occlusal wear in great ape mandibular deciduous fourth premolars (dp_4s)," I examine whether great ape dp_4s wear in

a manner that maintains occlusal topographic features. Using dental topographic analyses, I test the hypothesis that the occlusal features will be maintained, at least for a proportion of the dp_4 lifespan. The results of this chapter assist in deciphering whether dp_4 wear differences (or similarities) can be attributed to weaning, which is the focus of Chapter 3.

In Chapter 3, "Does wear on the mandibular fourth deciduous premolar (dp_4) demarcate age at weaning in the great apes?," I test Aiello et al.'s (1991) hypothesis that great apes species that wean earlier have greater dp_4 wear. While I test the hypothesis with a traditional measure of wear, percentage of dentine exposure, I also use more advanced techniques (i.e., dental topographic analyses). For life history data, I rely on the published literature.

In Chapter 4, "Body size, brain size, molar size, and the pace of dental development within the indriid-palaeopropithecid clade," I switch the discussion to lemurs. Since many lemurs are seasonal breeders, some with incredibly fast dental development, they offer an important perspective in contrast to the life history and dental developmental patterns of non-seasonal breeders, like the great apes. An exploration of the possible ecological scenarios primates have adapted to can assist paleoanthropologists when reconstructing life history profiles in extinct primate species. In Chapter 4, I present new molar developmental data for *Indri indri* and *Avahi laniger* using histological techniques. I explore the relationship between molar development and life history variables. Given the developmental connection between the timing of initiation among the primary postcanine dentition and tooth size, I also explore whether the molars in lemurs adhere to the inhibitory cascade (IC) model. I then apply the developmental concepts of the IC mechanism to life history data by assessing the relationships between

molar sizes and two life history variables (gestation length and age at weaning).

In Chapter 5, "Discussion," I summarize future research directions based on the results presented in the dissertation.

References

Aiello, LC, Montgomery, C, Dean, MC. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397–412.

Alqahtani, SJ., Hector, MP. Liversidge, HM. 2014. Accuracy of dental age estimation charts: Schour and Massler, Ubelaker and the London atlas. Am J Phys Anthropol 154:70-78.

Ankel-Simons, F. 2007. An introduction to primate anatomy. San Diego: Academic Press.

Ashton, EH., Zuckerman, S. 1950. Some quantitative dental characteristics of the chimpanzee, gorilla and orang-outang. Philos T R Soc B 234:471-484.

Baker, G., Jones, LHP. Wardrop, ID. 1959. Cause of wear in sheep's' teeth. Nature 184:1583-1584.

Bateson, P. 1994. The dynamics of parent-offspring relationships in mammals. Trends Ecol Evol 9:399-403.

Baume, LJ. 1950. Physiological tooth migration and its significance for the development of occlusion: I. The biogenetic course of the deciduous dentition. J of Dent Res 29:123-132.

Berkovitz, B., Moxham, B. J., Linden, R. Sloan, A. 2011. Master Dentistry (Volume 3). Edinburgh: Elsivier.

Berthaume, MA., Dumont, ER., Godfrey, LR. Grosse, IR. 2013. How does tooth cusp radius of curvature affect brittle food item processing? J R Soc Interface Journal of the Royal Society Interface 10:20130240.

Blanco, MB., Godfrey, LR. 2013. Does hibernation slow the "pace of life in dwarf lemurs (*Cheirogaleus spp.*)? Int J Primatol 34:130-147

Birch, W., Dean, C. 2009. Rates of enamel formation in human deciduous teeth. Front Oral Biol 13:116-120

Burkart, JM., Hrdy, SB. Van Schaik, CP 2009. Cooperative breeding and human cognitive evolution. Evol Anthropol 18:175-186.

Carlson, BA., Kingston, J. D. 2014. Chimpanzee isotopic ecology: A closed canopy C_3 template for hominin dietary reconstruction. J Hum Evol 76:107 - 115.

Catlett, KK., Schwartz, GT., Godfrey, LR. Jungers, WL 2010. "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. Am J Phys Anthropol 142:391-404.

Cerling, TE., Chritz, KL., Jablonski, NG., Leakey, MG. Manthi, FK. 2013. Diet of *Theropithecus* from 4 to 1 ma in Kenya. Proc Natl Acad Sci 110:10507-10512.

Chai, H., Lee, JJ., Constantino, PJ., Lucas, PW. Lawn, BR. 2009. Remarkable resilience of teeth. Proc Natl Acad Sci USA 106:7289-7293.

Constantino, PJ., Lee, JJW., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, BR. 2012. The role of tooth enamel mechanical properties in primate dietary adaptation. Am J Phys Anthropol 148:171-177.

Cuozzo, FP., Sauther, ML. 2012. What is dental ecology? Am J Phys Anthropol 148:163-170.

Dart, RA. 1925. *Australopithecus africanus*: The man-ape of South Africa. Nature 195-199.

Dart, RA. 1948. The adolescent mandible of *Australopithecus prometheus.* Am J Phys Anthropol 6:391-412.

Dean, MC., Leakey, MG. 2004. Enamel and dentine development and the life history profile of *Victoriapithecus macinnesi* from Maboko Island, Kenya. Annals of Anatomy 186:405-412.

Dean, MC, Wood, BA. 1981. Developing pongid dentition and its use for aging individual crania in comparative cross-sectional growth studies. Folia Primatol 36 (1-2): 111–27.

Dean, C., Leakey, MG., Reid, D., Schrenk, F., Schwartz, GT., Stringer, C. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414:628-631.

Dirks, W., Humphrey, LT., Dean, MC. Jeffries, TE. 2010. The relationship of accentuated lines in enamel to weaning stress in juvenile baboons (*Papio hamadryas anubis*). Folia Primatol 81:207-223.

El Aidi, H., Bronkhorst, E. M. Truin, G. J. et al. 2008. A longitudinal study of tooth erosion in adolescents. Journal of Dental Research 87:731-735.

Elgart, AA. 2010. Dental wear, wear rate, and dental disease in the african apes. *Am* J of Primatol 71:1–11.

Evans, AR. 2013. Shape descriptors as ecometrics in dental ecology. Hystrix: the Italian Journal of Mammalogy 24:133-140.

Evans, AR, Daly, ES, Catlett, KK, Paul, KS, King, SJ, Skinner, MM, Nesse, HP, Hublin, JJ, Townsend, GC, Schwartz, GT, Jernvall, J. 2016. A simple rule governs the evolution and development of hominin tooth size. Nature 530: 477-480.

Galbany J, Romero A, Mayo-Alesón M, Itsoma F, Gamarra B, Pérez-Pérez A, Willaume E, Kappeler PM, Charpentier MJE. 2014. Age-related tooth wear differs between forest and savanna primates. PLoS One 9:e94938.

Glowacka, H, McFarlin, S., Catlett, KK., Mudakikawa, A., Bromage, TG., Cranfiled, MR., Stoinksi, TS., Schwartz, GT. In Press.. Molar wear in wild population of known-age mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol.

Godfrey, LR, Samonds, KE, Jungers, WL, and Sutherland, MR. 2003. Dental development primate life histories. in primate life histories and socioecology In: Kappeler, PM and Pereira, ME, editors. Chicago: University of Chicago, pp. 177–203.

Godfrey, LR., Samonds, KE., Jungers, WL., Sutherland, MR. Irwin, MT. 2004. Ontogenetic correlates of diet in Malagasy lemurs. Am J Phys Anthropol 123:250-276.

Godfrey, LR., Schwartz, GT., Samonds, KE., Jungers, WL. Catlett, KK. 2006. The secrets of lemur teeth. Evol Anthropol 15:142-154.

Godfrey, LR, Samonds , KE, Wright , PC, King, SJ. 2005. Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol (Basel). 76 2): 77–99.

Godfrey, LR., Winchester, JM., King, J., Boyer, DM. Jernvall, J. 2012. Dental topography indicates ecological contraction of lemur communities. Am J Phys Anthropol 148:215-227.

Hardin, AM., Legge, SS. 2013. Geographic variation in nonmetric dental traits of the deciduous molars of *Pan* and *Gorilla.* Int J Primatol 34:1000-1019.

Kennedy, GE. 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. J Hum Evol 48:123-145.

Kupczik, K., Lev-Tov, N. 2014. The adaptive significance of enamel loss in the mandibular incisors of cercopithecine primates (Mammalia: Cercopithecidae): A finite element modeling study. PLOS ONE 9:e97677.

Hawkes, K. 2006. Life history theory and human evolution: A chronicle of ideas and findings. In: Hawkes, K., Paine, R. R., editors. The Evolution of Human Life History. pp 45–126

Hawkes, K., O'Connell, JF., Jones, NGB., Alvarez, H. Charnov, EL.1998. Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336-1339.

Hayssen, V. 1993. Empirical and theoretical constraints on the evolution of lactation. J Dairy Sci 76:3213-3233.

Hrdy, SB. 2009. Mothers and others: The evolutionary origins of mutual understanding. Harvard University Press: Belknap Press.

Howie, PW., Mcneilly, AS., Houston, MJ., Cook, A. Boyle, H. 1981. Effect of supplementary food on suckling patterns and ovarian activity during lactation. Brit Med J 283:757-759.

Ingicco, T., Moigne, A.-M. Gommery, D. 2012. A deciduous and permanent dental wear stage system for assessing the age of *Trachypithecus* sp. specimens (Colobinae, Primates). J Arch Sci 39:421-427.

Isler, K., Van Schaik, CP. 2012. Allomaternal care, life history and brain size evolution in mammals J Hum Evol 63:52-63.

Janis, CM, Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol Rev Camb Philos Soc 63 (2): 197–230.

Janson, CH., Van Schaik, CP. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira, ME., Fairbanks, LA., editors. Juvenile Primates: Life history, development, and behavior. Chicago: University of Chicago Press. pp 57–74.

Kaidonis, JA., Ranjitkar, SR., Lekkas, D., and Townsend, GC. 2012. An anthropological perspective: Another dimension to modern dental wear concepts. International Journal of Dentistry Volume 2012:1-2.

Kappeler, PM., Fichtel, C. 2012. A 15-Year Perspective on the Social Organization and Life History of Sifaka in Kirindy Forest. In: Kappeler, PM., Watts, DP., editors. Long-Term Field Studies of Primates. Springer Berlin Heidelberg. pp 101–121.

Kavanagh, KD, Evans, AR, Jernvall, J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449 (7161): 427–32.

Kay, RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195-216.

Kelley, J., Schwartz, GT. 2012. Life-history inference in the early hominins *Australopithecus* and *Paranthropus.* Int J Primatol 1-32.

Keown, AJ., Bush, MB., Ford, C., Lee, JJW., Constantino, PJ. Lawn, BR. 2012. Fracture susceptibility of worn teeth. J Mech Behav Biomed 5:247-256.

Kiliaridis, S. 2006. The importance of masticatory muscle function in dentofacial growth. Seminars in Orthodontics 12:110 - 119.

King, SJ, Arrigo-Nelson, SJ, Pochron, ST, Semprebon, GM, Godfrey , LR, Wright, PC, Jernvall, J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Aca Sci, USA 102 (46): 16579–83.

Kramer, KL. 2011. The evolution of human parental care and recruitment of juvenile help. Trends Ecol Evol 22:205-212. 26:533 - 540.

Kramer, KL., Russell, AF. 2015. Was monogamy a key step on the hominin road? Reevaluating the monogamy hypothesis in the evolution of cooperative breeding. Evol Anthropol 24:73-83.

Langer, P. 2008. The phases of maternal investment of eutherian mammals. Zoology 111:148-162.

Lathouwers, MD., Elsacker, LV. 2006. Comparing infant and juvenile behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): A preliminary study. Primates 47:287-293.

Lee, JJW., Constantino, PJ., Lucas, PW. Lawn, BR. 2011. Fracture in teeth-a diagnostic for inferring bite force and tooth function. Biol Rev 86:959-974.

Le Gros Clark, WE. 1947. Observations on the anatomy of the fossil australopithecinae. J Anat 83:300-333.

Lee, PC. 1996. The meanings of weaning: growth, lactation, and life history. Evol Anth 5:87-98.

Leigh, SR. 1994. Ontogenetic correlates of diet in anthropoid primates. Am J Phys Anthropol 94:499-522.

Lucas, PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press.

Lucas, PW., Casteren, AV., Al-Fadhalah, K., Almusallam, AS., Henry, AG., Michael, S. 2014. The role of dust, grit and phytoliths in tooth wear. Annales Zoologici Fennici Annales Zoologici Fennici 51:143-152.

Lucas, PW, Corlett, RT, Luke, DA. 1986. Postcanine tooth size and diet in anthropoid primates. Zeitschrift fur Morphologies und Anthropologie 253–76.

Lucas, PW, Omar, R, Al-Fadhalah, K., Almusalla, AS, Henry, AG, Michael, S. Thai, LA, Watzke, J., Strait, DS, Atkins, AG. 2013. Mechanisms and causes of wear in tooth enamel: Implications for hominin diets. Journal of The Royal Society Interface 10:1-9.

Macchiarelli, R., Bondioli, L., Debenath, A., Mazurier, A., Tournepiche, J. F., Birch, W. Dean, MC. 2006. How Neanderthal molar teeth grew. Nature 444:748-751.

Macena, MCB., Tornisiello Katz, CR., Heimer, MV., De Oliveira E Silva, J. F. Costa, L. B. 2011. Space changes after premature loss of deciduous molars among Brazilian children. Am J Orthod Dentofac 140:771-778.

Mahoney, P. 2015. Dental fast track: Prenatal enamel growth, incisor eruption, and weaning in human infants. Am J Phys Anthropol 156:407-421.

Mandalaywala, TM., Higham, JP., Heistermann, M., Parker, KJ. Maestripieri, D. 2014. Physiological and behavioural responses to weaning conflict in free-ranging primate infants. Animal Behaviour 97:241-247.

Mahoney, P. 2015. Dental fast track: Prenatal enamel growth, incisor eruption, and weaning in human infants. Am J Phys Anthropol 156:407-421.

Mann, A. 1975. Paleodemographic aspects of the South African australopithecines. University of Pennsylvania, Philadelphia, USA.

McNeilly, AS., Tay, CCK. Glasier, A. 1994. Physiological mechanisms underlying lactational amenorrhea. Annals of the New York Academy of Sciences 709:145-155.

Metcalf, CJE., Pavard, S. 2007. Why evolutionary biologists should be demographers? Trends Ecol Evol 22:205-212.

Moimaz, SAS., Araújo, PC., Chiba, FY., Garbín, CAS. Saliba, NA. 2013. Prevalence of deciduous tooth erosion in childhood. Int J Dent Hygiene 11:226-230.

Nanci, A. 2013. Ten Cate's Oral Histology: Development, Structure, and Function (8 ed.). St. Louis: Elsevier Mosby.

Ohba, M., Samonds, KE., Lafleur, M., Ali, JR. Godfrey, LR. 2016. Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. Palaeogeogr Palaeocl 441:688-695.

Osborn, HF. 1907. Evolution of Mammalian Molar Teeth: To and From the Triangular Type Including Collected and Revised Researches Tritubercuy and New Sections on the Forms. (Biological Studies and Addresses. Vol. I). London: MacMillan.

Owen, R. 1840. Odontography; Or, a Treatise on the Comparative Anatomy of the Teeth; Their Physiological Relations, Mode of Development, and Microscopic Structure, in the Vertebrate Animals. By Richard Owen. Longon: Hippolyte Baillière.

Plavcan, JM. 2001. Sexual dimorphism in primate evolution. Yrbk Phys Anthropol Vol 44:25-53.

Plavcan, JM. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: Implications for the fossil record. Am J Phys Anthropol 120:38-60.

Rabenold, D, Pearson, OM. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. PLoS ONE 6 (12): e28379.

Reitsema, LJ. 2012. Introducing fecal stable isotope analysis in primate weaning studies. Am J Primatol 74:926-939.

Robson, SL., Van Schaik, CP. Hawkes, K. 2006. The derived features of human life history. In: Hawkes, K., Paine, R. R., editors. The evolution of human live history. Santa Fe: School of American Research Press. pp 17–44.

Roff, DA. 2002. Life history evolution. Sunderland, Massachusetts: Sinauer Associates, Inc.

Sanson, GD., Kerr, SA. Gross, KA. 2007. Do silica phytoliths really wear mammalian teeth? Am J Phys Anthropol 34:526-531.

Scott, RS., Teaford, MF. Ungar, PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Schoeninger, MJ. 2014. Stable isotope analyses and the evolution of human diets. Annu Rev Anthropol 43:413-430.

Schwartz, GT. 2012. Growth, development, and life history throughout the evolution of *Homo*. Curr Anthrolpol 53:S395-S408.

Schwartz, GT., Dean, MC. 2008. Charting the chronology of developing dentitions. In: Irish, JD., Nelson, GC., editors. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press. pp 219–233.

Schwartz, GT, Samonds, KE, Godfrey, LR, Jungers, WL, Simons, EL. 2002. Dentalmicrostructure and life history in subfossil Malagasy lemurs. Pro Natl Acad Sci, USA 99 (9): 6124–29.

Simpson, GG. 1936. Studies on the earliest mammalian dentition. Dental Cosmos 78: 791–800.

Smith, BH. 1989. Dental development as a measure of life history in primates. Evolution 43:683-688.

Smith, BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:134-142.

Smith, BH, Crummett, TL Brandt, KL. 1994. Ages of eruption of primate teeth: acompendium for aging individuals and comparing life histories. Yrbk Phys Anthropol 37 177–231.

Smith, CC., Morgan, ME. Pilbeam, D.2010. Isotopic ecology and dietary profiles of Liberian chimpanzees. J Hum Evol 58:43 - 55.

Smith, TM. 2013. Teeth and human life-history evolution. Annu Rev Anthropol 42:191-208.

Smith, TM., Machanda, Z., Bernard, AB., Donovan, RM., Papakyrikos, AM., Muller, MN, Wrangham, R. W.2013. First molar eruption, weaning, and life history in living wild chimpanzees. Proc Natl Acad Sci 110:2787-2791.

Smith, TM., Tafforeau, P., Reid, DJ., Grun, R., Eggins, S., Boutakiout, M. Hublin, J-J. 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci U S A 104:6128-6133.

Sponheimer, M., Alemseged, Z., Cerling, TE., Grine, FE., Kimbel, WH., Leakey, MG. Lee-Thorp, JA, Manth, FK, Reed, KE, Wood, BA, Wynn, JG. 2013. Isotopic evidence of early hominin diets. Proc Natl Acad Sci, USA 110:10513-10518.

Stearns, SC. 1992. The evolution of life histories. New York: Oxford.

Stewart, KJ. 1988. Suckling and lactational anestrus in wild gorilla (*Gorilla gorilla*). J Reprod Fertil 83:627-634.

Swindler, DR. 2002. Primate dentition: An introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

Tanaka, EM., Sato, S. 2008. Longitudinal alteration of the occlusal plane and development of different dentoskeletal frames during growth. Am J Orthod Dentofac 134:602.e1-602.e11.

Teaford, MF. 1988. A review of dental microwear and diet in modern mammals. Scanning Microsc 2:1149-1166.

Teaford, MF., Ungar, PS. 2000. Diet and the evolution of the earliest human ancestors. Pro Natl Acad Sci USA 97:13506-13511.

Thompson, ME. 2013. Comparative Reproductive Energetics of Human and Nonhuman Primates. In: Brenneis, D., Strier, KB., editors. 42. pp 287–304

Thompson, ME., Müller, MN. Wrangham, RW. 2012. The energetics of lactation and the return to fecundity in wild chimpanzees. Behav Ecology 23:1234-1241.

Trivers, R. L. 1974. Parent-offspring conflict. Am Zool 14:249-264.

Trotter, M., Hixon, BB. Macdonald, BJ. 1977. Development and size of the teeth of *Macaca mulatta.* Am J Anat 150:109-127.

Ungar, PS. 2010. Mammal Teeth: Origin, Evolution, and Diversity. Baltimore: The John Hopkins University Press.

Ungar, PS, M'Kirera, F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proc Natl Acad Sci, USA* 100 (7): 3874–77.

van Noordwijk., Kuzawa , MA., van Schaik, CP. 2013. The evolution of the patterning of human lactation: a comparative perspective. Evol Anthropol 22:202-212.

Vitzthum, VJ. 1994. Comparative study of breastfeeding structure and its relation to human reproductive ecology. Yrb Phys Anthropol 37:307-349.

Walker, A., Hoeck, HN. Perez, L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201:908-910.

Williams, GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:411-398.

Wright, PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Am J Phys Anthropol Suppl 29:31-72.

Yamashita, N., Cuozzo, FP. Sauther, ML. 2012. Interpreting food processing through dietary mechanical properties: A lemur catta case study. Am J Phys Anthropol 148:205-214.

Zehr, SM., Roach, RG., Haring, D., Taylor, J., Cameron, FH. Yoder, AD. 2014. Life history profiles for 27 strepsirrhine primate taxa generated using captive data from the duke lemur center. Sci Data 1:140019.

Zihlman, A., Bolter, D. Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. Proc Natl Acad Sci USA 101:10541-10543.

CHAPTER 2

DENTAL TOPOGRAPHIC ANALYSES OF OCCLUSAL WEAR IN GREAT APE MANDIBULAR DECIDUOUS FOURTH PREMOLARS (DP_4S).

Abstract

Objectives: Great ape deciduous teeth remain in functional occlusal for several years; however, it is unknown whether deciduous teeth wear in manner that maintains occlusal topographic features. This study tests whether the occlusal terrain is preserved for at least a proportion of the dp_4's lifespan.

Material and Methods: High-resolution molds of dp_4s (N=278) from six species of great ape were collected at various museums. Casts were scanned and analyzed using dental topographic analyses. Changes over time in occlusal gradients (slope) and other measures of occlusal terrain (angularity, relief index, and orientation patch counts rotated (OPCRs) were analyzed using linear and segmented regressions. Segmented regressions enable the identification of biologically meaningful breakpoints in the predictor variables, which in this case were dental developmental scores (i.e., a proxy for age). AICcs were used to determine the best-fitting regression model. Dentine exposure, a measure for tissue loss, was also analyzed.

Results: With the exception of *Pongo pygmaeus*, all other species exhibited evidence of occlusal topographic maintenance for at least one of the variables. With the exception of *P. pygmaeus*, evidence of complexity (OPCR) maintenance was observed for all other species. For most comparisons, linear models were the best fit. When segmented regressions were the best fit, breakpoints occurred primarily before or during the emergence of the M_2.

Discussion: This study suggests that mechanisms are in place to preserve occlusal complexity throughout dp_4 wear. There is also evidence that the subsequent

emergence of molars, particularly the M_2, mitigate the effects of dp_4 wear in some great ape species. Future research directions are discussed.

Introduction

Teeth are adapted to meet the functional demands of various dietary regimes (e.g., Owen, 1840; Osborn, 1907; Simpson, 1936; Kay, 1975; Lucas et al., 1986; Teaford, 2000; Ungar, 2010). Dental features (e.g., hardness, enamel thickness, occlusal area) that allow teeth to effectively process particular diets are the same properties that enable teeth to counteract the irreversible effects of wear (Janis and Fortelius, 1988; Lucas, 2004). Mechanisms that mitigate tooth wear are important because wear eventually removes dental tissue, and this is particularly detrimental to enamel because this tissue lacks the ability to regenerate itself (e.g., Hillson 2003; Nanci, 2013; Borrero-Lopez et al. 2014). Selective pressures from food mechanical properties have acted on tooth shape, which includes the occlusal terrain (Lucas et al. 1986; Lucas 2004). As the occlusal surface wears, the enamel and associated morphological features (e.g., cusps, shearing crests, ridges, crenulations) disappear, modifying and reshaping the entire occlusal terrain throughout wear. Concomitant tissue loss and modification of the occlusal surface does not automatically qualify these changes as a disadvantage. For example, shearing crests may maintain, or even increase, throughout wear despite the loss of dental tissues, as evidenced by greater proportions of dentine exposure over time (e.g., King et al., 2005; Glowacka et al., In Press). A wear-pattern that maintains shearing capacity is advantageous for primates that eat tough diets because it enables the tooth to maintain a degree of functional efficiency throughout a large proportion of the animal's lifespan. Studies on other non-primate mammals found that molars wear in a manner that maintains functional

efficiency until late stages of life (e.g., Gipps and Sanson 1984; Janis and Fortelius 1988; Veiberg et al. 2007).

To quantify how the occlusal terrain reshapes throughout wear, it is necessary to analyze these changes using 3D technologies, as this approach enables the application of spatial statistical analyses (e.g., Ungar and Williamson, 2000; Wheatley and Gillings, 2002; Dale, 2005). Recently, several researchers amalgamated the field of dental anthropology with geographical information systems (GIS) software to create a new methodology for analyzing complex occlusal surfaces—dental topographic analyses (Zuccotti et al., 1998; Ungar and Williamson, 2000; Evans et al., 2007; Boyer, 2008; Bunn et al., 2011). Dental topographic analyses are currently employed for two main types of studies: those that seek to segregate species into broad dietary categories and those that quantify complex occlusal wear patterns (e.g., Dennis et al., 2004; Ungar et al. 2004; Evans et al. 2007; Winchester et al., 2014). Dental topographic analyses are relatively new and continually being refined; however, this is currently the preferred method to test whether wear remodels occlusal surfaces to maintain terrain complexity. Maintenance of the occlusal terrain suggests preservation of functional efficiency despite the loss of dental tissues. Functional efficiency implies that the tooth will maintain qualities that mitigate the effects of wear (e.g., maximize durability, generate compensatory shearing blades) to minimize the energy required to breakdown foods. Measuring the size of fecal particles or counting chewing cycles are additional ways to indirectly measure a tooth's functional efficiency (e.g. Prinz and Lucas, 1997; Millette et al., 2012; Matsuda et al., 2014; Venkataraman, et al. 2014). An important point to note is that maintenance of occlusal topographic features does not necessarily mean the maintenance of *optimal* functional efficiency. Rather, maintenance refers to a pattern where dental

topographic values are sustained for at least a proportion of the tooth's overall lifespan, which, in turn, would preserve a morphologically diverse surface (e.g., cusps, shearing blades) that can effectively masticate foods.

The application of dental topographic analyses to the primate dentition has yielded several interesting, but mixed, results. Although broad taxonomic comparisons are lacking, very broad generalizations are emerging. Primates that subsist on more folivorous or graminivorous diets tend to maintain occlusal jaggedness and shearing reliefs (e.g., Ungar and Williamson, 2000; Dennis et al., 2004; King et al., 2005; Venkataraman et al., 2014; Glowacak et al., In Press). Available data for primates that subsist on more frugivorous diets are equivocal. For example, some chimpanzee species or populations may preserve occlusal complexity (e.g., Ungar and M'Kiera, 2003), and other *Pan* groups do not (e.g., Klukkert et al., 2012). In addition, dental topographic data collected from different tooth positions do not necessarily produce the same wear pattern, as evidenced when Bunn and Ungar (2009) documented that the M_1 and M_2 produced non-interchangeable results. As dental topographic data sets grow and intra-and interspecific wear variation is observed, the possibility of linking wear patterns to ecological factors increases (e.g., Venkataraman et al., 2014; Cuozzo et al., 2014); however, notably absent from dental topographic analyses is the inclusion of primate deciduous teeth. Specifically, information is lacking on whether primate deciduous teeth wear in a manner that maintains occlusal topography and, by proxy, an aspect of a tooth's overall functional efficiency.

Similar to many other mammalian orders[1], Primates possess two sets of dentition that are commonly labeled as the deciduous and permanent teeth. The deciduous dentition comprises incisors, canines, and premolars. In many bioarchaeological or human clinical settings, the deciduous premolars are referred to as the deciduous molars; however, within a developmental context, primates only develop one set of molars, which are often referred to as permanent molars (e.g., reviewed by: Swindler, 2002; Hillson, 2003; 2005; Ungar, 2010). To reflect the developmental progression of the dentition, this study refers to the most distal deciduous tooth-type as deciduous premolars; however, the developmental relationship between deciduous premolars and molars is more than pedantic parlance. Controlled experiments established the presence of an inhibitory cascade among adjacently developing teeth and discovered how the ratio of inhibitor and activator molecules influence subsequently developing posterior teeth in both the timing of tooth initiation and overall tooth size (Kavanagh et al. 2007). Follow-up studies have examined the developmental relationship among the deciduous, succedaneous, and molar dentitions (Jarvinen et al. 2008; Atsushi et al., 2010; Schroer and Wood, 2015). Evans et al. (2016) applied the inhibitory cascade model to the mandibular primary postcanine dentition (i.e., deciduous premolars and molars) in great apes, humans, and hominins and found that it held, indicating that the size and developmental timing of the postcanine deciduous teeth could affect the M_1 and, in turn, subsequently developing mandibular molars. Therefore, selection acting on the deciduous teeth may affect molar development, suggesting that investigation into the functional role of the deciduous teeth is warranted.

[1] While the possession of a diphyodont dentition is a mammalian synaopmorphy, there are many examples where species either do not develop the deciduous dentition (e.g., mice), or they develop multiple sets of teeth that are replaced (e.g., elephants) (Hillson, 2005; Ungar, 2010).

Relative to the permanent teeth, the deciduous dentition is reduced in size, and this enables smaller, but growing, jaws to maintain proper occlusion (e.g., Baume, 1950). Neglect of the deciduous teeth, such as through poor hygiene practices, or premature exfoliation (e.g., trauma) may affect proper dental development (e.g., Macena et al., 2011; Nanci, 2013). Masticatory forces, induced via chewing or teething, also play an important role in generating proper craniofacial development, as it affects bone growth (e.g., Kiliaridis, 2006; Tanaka and Sato, 2008). Schwartz (2012) reports that in modern humans the timing of postcanine tooth emergence, including the deciduous premolars, coincides with cranial growth in a manner that maintains biomechanical optima relative to the temporomandibular joint, masticatory musculature, and occlusal bite points. These results suggest that strong selective pressures constrain the timing of primary postcanine dental emergence with craniofacial development.

In comparison to the succedaneous dentition, primary teeth develop faster, as they must attain functional occlusion within a shorter timeframe. Therefore, the proportion of enamel and dentine that develops prior to birth tends to exhibit accelerated enamel, dentine, and root growth rates (e.g., Macchiarelli et al., 2006, Birch and Dean, 2009; Mahoney, 2015). In primates, a large proportion of the deciduous dentition (e.g., complete crowns) is fully developed at birth (Smith et al., 1994; Swindler, 2002), and in some strepsirrhine primates, extensive M1 and even M2 development is observed (Schwartz et al., 2002; Godfrey et al., 2006; Catlett et al., 2010; Chapter 4). However, the functional contribution of deciduous teeth appears to vary among primate species. In primates with extremely fast dental development (e.g., indriids), the deciduous teeth shed very quickly and, in some primates, such as tarsiers, the deciduous teeth shed *in utero* and can even be considered vestigial (Smith

et al. 1994; Schwartz et al. 2002; Godfrey et al. 2005). Metabolic factors can vary the rate of dental development, such as when mouse lemurs undergo seasonal torpor (Blanco and Godfrey, 2013). In contrast to lemurs, species with much longer dental developmental schedules, such as the great apes, the deciduous dentition is retained for several years and remains in functional occlusion both before and after the multiyear process of weaning (Dean and Wood 1981; Aiello et al. 1991; Smith et al. 1994; Chapter 3).

As previously mentioned, the dentition utilizes a variety of means to resist wear. These mechanisms include properties such as tissue hardness, enamel thickness, and decussating enamel (e.g., Janis and Fortelius, 1988; Lucas, 2004; Shimizu and Macho, 2008; Chai et al., 2009). While there is a paucity of literature, presumably the primate deciduous dentition employs similar mechanisms as molars to mitigate the irreversible loss of enamel. Darnell and colleagues (2010) compared the mechanical properties of a maxillary deciduous fourth premolar (dp^4) to maxillary first and third molars (M^1 and M^3, respectively) from a Central American howler monkey (*Alouatta palliata*). Although the dp^4 was worn, Darnell et al. (2010) found that the distribution of enamel hardness was on par with the M^1 and M^3 in this individual, suggesting that despite the dp4s' smaller size and likely faster growth rates, deciduous premolars are likely to be as structurally sound as molars. Broad interspecific studies are also lacking on enamel thickness in primate deciduous teeth; however, the data presently available indicate dp4s have the thickest enamel among deciduous teeth, but when compared to the molars, dp4s have reduced enamel thickness values, potentially limiting their functional longevity (Aiello et al. 1991; Grine, 2005; Mahoney, 2013).

The wide variation in primate deciduous tooth development and shedding schedules may reflect different biological functions in the deciduous dentition (e.g.,

extensively active in digestion or a short-term placeholder for the succedaneous teeth). The biological part deciduous teeth play in a juvenile is, at least partially, dependent upon the socioecological setting (e.g., Altmann, 1991; Godfrey et al., 2003). Juvenile primates must mitigate many costs as they allocate energy to growth and development, hone newly acquired foraging skills, and avoid predators (e.g., Janson and van Schaik, 1993). As previously discussed in Chapter 1, tooth wear provides a record of how the teeth interacted with the environment (e.g., Cuozzo and Sauther, 2012). Studying primate deciduous tooth wear can provide insight into how juvenile primates interacted with their ecological settings while simultaneously limiting mortality risks to, eventually, become reproductively fit individuals. Given this broad functional and developmental variation, dental topographic analyses of deciduous teeth suggest a promising route to unravel how selection may act on deciduous tooth occlusal wear.

Hypotheses

This study tests the hypothesis that, at least for a time, the occlusal features on great ape mandibular dp_4s will be maintained. Specifically, measures of overall gradient (i.e., slope; see Methods) should decline with no evidence of maintenance. Tissue loss (i.e., dentine exposure; see Methods) should increase with no evidence of maintenance. Other measures that assess occlusal terrain, such as projections of relief and overall complexity, should be maintained, at least for a proportion of the dp_4s' lifespan. Since great apes utilize deciduous teeth longer than any other nonhuman primate species (e.g., Aiello et al., 1991; Smith et al., 1994), they are an ideal group to assess deciduous tooth wear patterns. The presence of occlusal maintenance may indicate broader evolutionary implications regarding the evolution of dp_4 occlusal

morphology. Evidence of maintenance suggests the possibility that selection may act on how dp_4s wear, in a manner similarly observed in the molars of some primate species (e.g., Ungar and M'Kiera, 2003; King et al., 2005).

Material and Methods

Sample

Table 2.1 presents sample sizes for each taxon (N=278). High quality, dental impression molds were collected from mandibular dp_4s attributed to six great apes species: *Gorilla beringei*, *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, *Pongo pygmaeus*, and *Pongo abelii*. Due to small samples, no distinction was made between the *G. beringei* subspecies; therefore, specimens belonging to *G. b. beringei* and *G. b. graueri* were pooled and analyzed as one species, *G. beringei* (Table 2.1). Hardin and Legge's (2013) work on nonmetric variation in African great ape deciduous premolars found that great ape populations more genetically related share similar nonmetric dental traits. While their study did not include *G. b. beringei*, they did note the presence of greater interspecific variation than comparisons of sub-specific variation (e.g., in *Pan* subspecies). Therefore, pooling the *G. beringei* subspecies in this study should not overly affect the results. Utilizing dental topographic analyses, Klukkert et al.'s (2012) comparison of wear on the M_2 among three different subspecies of chimpanzees yielded no significant differences. Sample sizes permitted separate analyses of the dp_4s from two chimpanzee subspecies, *P. t. schweinfurthii* and *P.t. troglodytes* (Table 2.1). This allowed an assessment as to whether the dp_4s follow the same wear pattern that Klukkert et al (2012) observed in the M_2s of chimpanzee subspecies.

Specimens analyzed are housed at the Natural History Museum, Cleveland,

American Museum of Natural History, New York, National Museum of Natural History, Washington D.C., Museum of Comparative Zoology, Cambridge, Powell-Cotton Museum, Birchington-by-the-Sea, Zoological Museum, Munich, Natural History Museum Brussels, Royal Museum of Central Africa, Tervuren, and University of Anthropology, Zurich (Appendix A). To ensure that the tooth wear analyzed stemmed from a 'natural' biological setting, museum records were used to determine whether individuals were wild-shot or captive. Captive animals usually feed on processed foods and engage in abnormal chewing behaviors (e.g., gnawing on cages); these factors can affect the state of tooth wear (e.g., Bayne and Turner, 2014). Therefore, with the exception of three individuals, all dp_4s are from specimens that were wild-shot or died in their natural habitat. For the three non-wild individuals, one belongs to *P. abelii* and the other two belong to *P. pygmaeus*. All three captive individuals were very young and their newly emerged dp_4s were retained in the sample to represent the unworn, pristine condition. For many of the youngest individuals, sex was unknown; therefore, sexes were pooled for analysis.

Using a digital SLR camera and macro lens (Canon, U.S.A.), each specimen was photographed in both .raw and .jpg formats. Mandibles were secured to a portable copy stand using clay. Both the occlusal plane of the dp_4 and the camera were positioned in the same plane using levels. Light sources were covered with white tissue paper to ensure an evenly lit occlusal surface, and a remote camera switch was used to maximize image clarity. These images were later used to measure dentine exposure (see below).

Standard molding and casting materials and methods were utilized to produce high fidelity replicas of the occlusal surfaces (e.g., Ungar and M'Kirera, 2003; King et al., 2005). High-resolution molds were collected using President Jet Plus (Light

Body), a polyvinylsiloxane-based impression material used in clinical settings to produce high precision dental restorations. For each dp_4, the President Jet Plus material was first painted on the occlusal surface using a spot touch taklon bristled brush (sizes: 5/0 and 10/0). Taklon is a synthetic fiber that is less absorbent than natural hair and allowed an easier application of the molding material to the occlusal surface. This technique, developed by Stroik (2014), minimized the presence of air bubbles and helped ensure that fine occlusal details were fully captured during the molding process. After molding material was painted on the occlusal surface, a President Jet Cartridge Dispenser was used to mold the entire tooth crown. Dried molds were then carefully removed from museum specimens by hand.

Before pouring, molds were stabilized by using silicone impression putty (Coltoflax) to form a base. High-quality casts were crafted using Fujirock, a gypsum-based die stone that produces high quality, durable stone models. One technique to minimize the formation of bubbles when pouring the casts is to reduce the surface tension. Therefore, a small amount (i.e. ~2 drops for ~6-8 oz. of wet molding material) of isopropyl alcohol (70%) was added to the wet molding mixture (i.e., distilled water and the Fujirock), which was stirred ~20-30 seconds on a vibrating plate (Vibrator, Henry Schein). The casts were then poured. Dried casts were carefully extracted from the molds by hand and assessed to ensure the occlusal surface was faithfully replicated. Suitable casts were then scanned.

The occlusal surfaces of the casts were digitized in the xyz planes using the Roland Active Piezo Sensory Probe of a Roland MDX-15 Scanning and Milling Machine at the maximum resolution available, $50\mu m$. Each tooth was secured to the MDX-15 table using clay and was mesiodistally oriented along the y-axis. The positioning of the occlusal plane for each tooth was visually assessed to ensure that

the entire dp_4 occlusal surface was level prior to scanning. The point cloud data were saved as .txt files (xyz coordinates) and then exported to geographic information systems (GIS) and mapping programs (i.e., GRASS GIS v. 7.0 and Surfer v. 8.0).

Data Acquisition

GRASS GIS is a powerful open source program that enables the simultaneous analysis, visualization, and storage of complex spatial and geographical data in both raster and vector formats. GRASS GIS was used to process and collect most of the data for this study. Data for one variable, orientation patch counts rotated (see below), was collected in Surfer (Golden Software, LLC.) using a module (Surfer Manipulator) developed by Evans et al. (2007). Mapping software, like Surfer, can also digitally recreate spatial data, as well as conduct a limited set of complex spatial analyses.

From the .txt file, two sets of raster-based digital elevation models (DEMs) were generated, one in GRASS GIS and another in Surfer. Broadly defined, DEMs are digital reconstructions of the terrain (Wheatley and Gillings, 2002). DEMs are used for statistical spatial analyses of geographical data in GIS and other mapping software programs (Conolly and Lake, 2012). Here, scanned occlusal surfaces were reconstructed as DEMS. In GRASS GIS, DEMs were constructed using the r.in.xyz module. A python script was written to automate the task (Appendix B). Following similar approaches outlined in Klukkert and colleagues (2012), the extent of the occlusal surface for each DEM measured was determined by locating the inferiormost point deep within the occlusal basin. This point was then set at the lower limit and all coordinate data below that point within the occlusal outline were then eliminated using the raster calculator in GRASS GIS. Following the principles outlined by Boyer (2008), each cropped DEM was smoothed to account for any unrealistic surface

representations in the digital reconstruction. Each DEM was smoothed in the GRASS GIS r.neighbors module. A script written in Python was used to automate this process to ensure that each tooth underwent the same smoothing transformation process (Appendix B).

Following procedures outlined by Evans and colleagues (2007), raster-based DEMs were also generated and cropped using Surfer Manipulator. Occlusal outlines of each DEM were digitzed and excess data were removed. The cropped DEMs were smoothed by constraining each occlusal surface to a 50x50 grid, which followed previously defined protocols (e.g., Evans et al., 2007; Evans and Janis, 2014). All subsequent data collection and analyses were based off the cropped, smoothed DEMs.

Four standard dental topographic variables were analyzed for this study: slope (mean), angularity (mean), relief index (RFI), and orientated patch counts rotated (OPCRs). Figure 2.1 summarizes the variables analyzed in this study. Slope is the mean gradient for the overall occlusal surface and is useful for assessing how a smooth or rough terrain changes over time (Ungar and Williamson, 2000). Only terrain slopes 5 degrees or greater relative to the lowest point in the occlusal basin were measured, a common cutoff point (Ungar, 2007). Angularity is another global measure of a terrain's jaggedness but it incorporates the rate of change in the slope across the occlusal surface (Ungar and Williamson, 2000). In other words, it is a measure of how quickly or slowly the occlusal surface gradient changes across a designated “landscape” (i.e., the occlusal surface). Both slope and angularity are reported in degrees. Since an individual occlusal surface possesses several slopes and gradient changes, the mean slope and mean angularity for each occlusal surface were the values recorded. RFI is a measure of the overall projection of the occlusal surface and is the ratio of the 3D and 2D surface area (Ungar and Williamson, 2000; King et

al., 2005). Python scripts automated data collection in GRASS GIS for slope, angularity, and relief index (Appendix B). The Python scripts improved both data collection efficiency and repeatability for each tooth.

The PDE (percentage of dentine exposure), a standard variable to assess 2D wear, was also calculated using GRASS GIS. Both the digital images and casts were referenced to determine the presence of dentine exposure. Areas of dentine exposure were digitized on the GRASS DEM and were saved as vector maps, which were then converted to 2D raster maps (v.to.rast module). Surface area data were collected using the r.surf.area module in Grass GIS. The percentage of dentine was calculated as (2D surface area of digitized regions/the total 2D surface area of the occlusal surface) *100. The same 2D surface area value used to calculate RFI was used in the calculation of the PDE.

OPCR data were collected in Surfer Manipulator (Evans et al., 2007; Evans and Jernvall, 2009; Evans and Janis, 2014). OPCR data are collected from aspect maps where the terrain is reclassified to represent the eight cardinal directions (e.g., north, northwest, west). Groups of at least three or more adjacent patches that face the same direction and were at an incline of at least 5 degrees relative to the occlusal plane were categorized as a 'dental tool'. These tools are then summed to produce an orientation patch count, which represents the number of 'dental tools' available on that occlusal surface (Evans et al., 2007). To account for potential variation in how the occlusal plane was defined, Surfer Manipulator employs an algorithm that tilts the scan eight times at ~5.63 degree increments, and the final OPCR value is the mean of the eight OPCR counts (Evans and Jernvall, 2009; Evans et al., 2014).

Relative Aging Methods

As absolute ages are generally not available for museum specimens, each individual was assigned a proxy age score based on the expected normal state of maxillary and mandibular dental development. In the great apes, the complete deciduous dentition comprises 20 teeth, and the permanent dentition comprises 32 teeth, for a grand total of 52 possible teeth for each individual. Using methods similar to Godfrey et al. (2003) and King (2004), each tooth was assigned a number based on its emergence status relative to the alveolar bone (Table 2.2). These scores were summed and divided by the maximum dental score possible (i.e., 208), yielding a value that represented the proportion of dental development completed for that individual. The dentition can be divided into four quadrants. Under conditions of normal dental development, an adult specimen with teeth fully emerged to the occlusal plane would have had five deciduous teeth and eight permanent teeth for each quadrant (i.e., 13 teeth) with a maximum dental score of 52 for that quadrant, or 52*4 for the entire dentition (i.e., 208). In this instance, each quadrant's score reflects the completed development, emergence, and subsequent exfoliation of the deciduous dentition. Therefore, for an adult specimen, the dental score, (i.e., proxy for relative age), is calculated as: (specimen's dental score/total possible dental score = relative age of that individual) (e.g., (208 /208 = 1.0). Multiplying a relative age by 100 yields a percentage. Therefore, a relative age of 0.62 is equivalent to stating that 62% of dental development is completed. Missing teeth were scored based on available antimeres within the same arcade. Individuals were seriated based on their dental scores, assuming the youngest individuals had the lowest dental scores. Table 2.1 summarizes the relative age ranges for each taxon.

Analytical Methods

Paleoanthropologists have found high correlations among the different dental topographic variables in molars (E.g., Bunn et al., 2011; Winchester et al., 2014; Glowacak et al., In Press); therefore, this study also assessed the degree of correlation among the variables for the great ape dp_4s. Correlation matrices were generated in R using the Kendall package (McLeod, 2011). The nonparametric test statistic, Kendall's tau, was chosen to assess association among the variables. Kendall's tau is similar to the more famous Spearman's rho, as they are both nonparametric alternatives to the Pearson-correlation coefficient. However, Kendall's tau was selected for this study as it is a preferred method for small sample sizes and reduces the effects of ties in ranked data (Field, 2009). Kendall's tau may also provide a better estimator for the population than compared to Spearman's rho (Daniel, 2000; Field, 2009). For the purposes of this study, each species and variable were analyzed separately; therefore, the correlation tests act more as a guide to understand the relationship of the five wear variables within each considered taxon, rather than testing specific hypotheses about those relationships.

Many researchers use categories (e.g., age ranges, wear stages) to bin individuals into discrete groups (e.g., King et al., 2005; Bunn and Ungar 2009; Klukkert et al., 2012). This is a useful approach, particularly when there is an overarching biological principle that can dictate how groups should be divided (e.g., immature vs. reproductively mature individuals, predefined states of wear, dietary categories); however, this was not the case for this study. Since great apes exhibit different absolute rates of dental development (reviewed in Chapter 3), allocating the great apes into discrete bins based on dental development (e.g., molar emergence) would have resulted in uneven bins across the species. In addition, teeth do not

necessarily wear in a uniform and linear fashion (e.g. Galbany, 2011). This presents a conundrum because commonly employed data transformation techniques used to account for scale differences or to mitigate problems associated with violated parametric statistical assumptions often involve applying a log transformation (e.g., Sokal and Rohlf, 1994). Unfortunately, log transformations or only applying linear regressions could obscure any potential nonlinear relationships, which might mask evidence of occlusal topographic maintenance. To overcome these obstacles, this study used both linear and segmented regression models.

Segmented regression models, also referred to as piecewise linear regressions, are used to detect potential directional changes (i.e., breakpoints) in the data (Muggeo, 2003; Segura et al., 2013). There are two key benefits of using segmented regression models over other nonlinear methods (e.g., splines or polynomials). Firstly, it is unnecessary to estimate *a priori* the point at which the linear slope changes; secondly, this approach does not artificially smooth a nonlinear line, which could ignore a potentially biologically meaningful breakpoint (reviewed by Muggeo, 2003). For example, if occlusal maintenance were present for at least a proportion of time within a dental wear series, segmented regression models would detect both the presence of maintenance and the point in time that occlusal maintenance started or ended. Therefore, for each individual taxon and variable, two regression analyses were conducted—linear and segmented regressions. In order to determine which regression method was best, this study used the Corrected Akaike Information Criterion (AICc). AICc is a standard technique that allows researchers to decide which of the examined models best fit the data when working with small sample sizes. AICc is a statistical method that utilizes a distance parameter calculated among the considered models that is then compared against the estimated log-likelihood maximum distance; therefore, it

is the difference in AICc values that researchers want to compare (Burnham and Anderson, 2002). The smaller AICc value is the preferred model, and, following standard protocols, this study considered comparisons that yielded a difference greater than two AICc units 'significant' (Burnham and Anderson, 2002; e.g., Segura et al., 2013). AICc weights (*w*) were also evaluated, as they report the probability of which model is best. The models with the higher probabilities are more likely to be the best models, and they correspond with the smaller AICc values. Statistical analyses were conducted in R-Studio (2015). The 'segmented' package (Muggeo, 2008) was used to generate segmented regressions, and the 'MuMIn" (Bartoń, 2015) package was used to conduct AICc analyses (Appendix C). As the segmented package utilizes a pseudo-randomization technique, the seed was set to 50 (Appendix C).

Testing the Hypothesis

This study tested whether occlusal features were maintained, even for a proportion of time, throughout wear. Therefore, after consulting the AICc output, the slopes (i.e., βs) for the best model—linear or segmented—were interpreted. βs equal to zero indicated the presence of occlusal maintenance, βs greater than zero suggested an increase in occlusal topographic features, and βs less than zero suggested that the occlusal topographic features declined. These criteria are summarized in Table 2.3. Interpretations of βs generated from linear regressions were based on whether βs were significantly different from zero. Interpretations for βs generated from segmented regressions were based on whether zero was included within the 95% confidence intervals; however, only βs that were significantly different, as determined by the Davies Test in the segmented package, were considered. Since multiple model types

were being compared, the adjusted R^2 values were reported. The adjusted R^2 accounts for the number of estimated parameters relative to sample size and is a more uniform assessment of variability when different types of models are being considered (Kutner et al. 2005; Field, 2009). Scatterplots of the best-fit models were plotted using the R graphics package, ggplot2 (Wickham, 2009; Appendix C).

An Assessment of Segmented Regressions for Occlusal Wear

Although segmented regressions are an established statistical technique, they have not been previously employed to analyze occlusal wear data. Therefore, both linear and segmented regressions were generated using King et al.'s (2005) published data set for their study on the M_2s from a wild population of highly folivorous sifakas, *Propithecus edwardsi.* The dental topographic variables they analyzed were relative crown relief and relative shearing blade lengths in both 2D and 3D, and they analyzed wear changes used binned aged groups. For relative crown relief, King et al. (2005) found that relief dramatically *decreased* between 6-12 years of age and remained mostly unchanged for the remaining years. Relative shearing blade lengths measured in 2D *increased* until dramatically decreasing at the late stages of life (i.e., age bin 18-27 years). Similarly, relative shearing blades measured in 3D were *maintained* until ~18-27 years of age. Given King et al.'s (2005) results (i.e., they reported directional changes in all three variables), it was expected that the segmented regressions would be the preferred model. Table 2.4 outlines interpretations for the βs based on King et al. (2005).

All the expectations were met. Tables 2.5 and 2.6 present the results for the linear and segmented regressions. As expected, AICcs indicated that the segmented regressions performed better than linear regressions for all three variables (Table 2.7),

as ΔAICc were > 2 and AICc ω favored the segmented regressions. King et al. (2005) detected crown relief changes in the binned age interval of 6-12 years. The segmented regression found a similar pattern (Table 2.6; Figure 2.2a). For relative crown relief, $\beta_1 < 0$, which suggests a decrease in relative crown relief, and β_2 included 0 within the 95% C.I., which suggests maintenance, or at least no change, in the relative crown relief. The breakpoints (BKs) indicate that the directional change of the βs occurs at ~8.4 years of age, which falls within King et al.'s (2005) binned age interval of 6-12 years.

For 2D relative shearing blade length, β_1 and the 95% C.I. were positive, suggesting that the relative length of the 2D shearing blades *increased* until ~13.05 years of age. After ~13 years of age, β_2 was < 0, indicating a reduction in the 2D shearing blades lengths (Table 2.6; Figure 2.2b). Interestingly, King et al. (2005) noted a dramatic decrease in 2D relative shearing blade length at the last age bin (i.e., 18-27 years of age); however, the overall pattern was an increase followed by a decrease in 2D relative shearing blade length (Table 2.6; Figure 2.2b). For 3D relative shearing blade length, the 95% C.I. for β_1 included 0, indicating maintenance of 3D relative shearing blade lengths. At ~13.4 years of age, the linear direction changed and β_2 was < 0, suggesting a decrease in occlusal topography (Table 2.6; Figure 2.2c). The expected wear pattern for 3D relative shearing length mirrored the one discovered by King et al. (2005); however, like the 2D shearing length crest result, the segmented regression for 3D shearing blade length estimated a slightly earlier age (i.e., ~13.40 years) of when blades start to decrease than King et al.'s (2005) age bin (i.e., 18-27 years). Given that segmented regressions replicated the broad interpretations for the King et al. (2005) data set, this regression technique seems to be a reasonable

approach to assess other forms of occlusal topographic data.

Results

Table 2.8 summarizes the ranges for all five variables. Along with sample sizes, Table 2.1 includes the relative age ranges for each taxon. Tables 2.9-2.11 present the mean and median relative ages for each species, which were converted into percentages to represent the proportion of complete dental development for each mandibular molar. *P. abelii* had the smallest sample (n=9; Table 2.1) and the narrowest representation of relative ages (~0.61 – 0.71; Table 2.1), which only represents ~10% of overall dental development (Tables 2.1 and 2.11); therefore, any interpretations of *P. abelii* dental wear are extremely tentative. Table 2.12 presents the results for all linear regressions, and Tables 2.13-2.17 summarize the segmented regression results for each species and variable; thus, a grand total of 70 regression analyses (i.e., 35 linear and 35 segmented) were compared. The AICc values, weights, differences, and best-predicted model outcomes are presented in Tables 2.18-2.22, and the conclusions are summarized in Table 2.23. For most species and variables, the linear regression was the preferred model. Scatterplots for the best-predicted models are presented in Figures 2.3-2.9 for each taxon. The resulting rank correlations (Kendall's tau) for occlusal topographic variables within each taxon are presented in Tables 2.24-2.30. For this specific study, each taxon and variable were considered separately and not compared statistically; hence, it was deemed unnecessary to apply a correction for pairwise comparisons or familywise error rates.

Slope

Slope measures the steepness, or gradient, of a surface, and it was predicted that slope would only decrease over time with no evidence of maintenance. The

prediction held for *G. beringei*, *P. paniscus*, *P. t. troglodytes*, and *P. pygmaeus*, as ΔAICc and AICc ωs indicated that the linear regressions with negative βs were the best-fit models (Table 2.18). Breakpoints were not estimated for *P. paniscus* and so, by default, the linear regression was determined to be the best model. For *P. pygmaeus,* the Davies Test indicated that the βs from the segmented regressions were not significantly different (Table 2.13); therefore, the linear regression was deemed the best fitting model for *P. pygmaeus*. In *P. abelii*, the slope was -3.08, but not significant ($p = 0.887$). Unexpectedly, segmented regressions were the best-fit models for *G. g. gorilla* and *P .t. schweinfurthii* (Table 2.18) and both species indicated evidence of maintaining slope values throughout wear. Both these species exhibited the same wear pattern, where slope first decreased (β_1) and then was maintained (β_2) (Figures 2.4a and 2.6a). The breakpoint occurred approximately at the same relative age in both species, 0.71 (Table 2.13).

Angularity

Angularity measures the jaggedness, or unevenness, of the surface, and in dental topographic studies is an assessment of the complexity of the occlusal surface. This study predicted that for measures of complexity there should be some evidence of maintenance. The prediction only held for *G. g. gorilla*, *P .t. schweinfurthii*, and *P. abelii* (Table 2.14). In *P. abelii*, angularity was maintained (i.e., $\beta = -0.843$, $p = 0.831$). Similar to the patterns observed for slope, segmented regressions were the best-fit models for *G. g. gorilla* and *P .t. schweinfurthii*, where β_1 decreased and β_2 maintained (i.e., 0 was included in the 95% C.I.) (Table 2.14; Figures 2.4b and 2.6b). The breakpoint occurred approximately at the same relative age in both species, 0.71-

0.72 (Table 2.14). The prediction did not hold for *G. beringei, P. paniscus, P. t. troglodytes,* or *P. pygmaeus*. ΔAICc values and AICc ωs for *G. beringei* and *P. paniscus* selected the linear regressions (-βs) as the preferred models (Table 2.19). For *P. t. troglodytes*, ΔAICc values were < 2 and the AICc ωs were nearly identical for both the linear and segmented regressions (Table 2.19); however, since the two predicted βs from the segmented regressions were not significantly different (Table 2.14), the linear regression was determined to be the preferred model. Breakpoints were not estimated for *P. pygmaeus* and so, by default, the linear regression was determined to be the best model.

RFI

RFI measures the overall 3D projection of the occlusal surface relative to the 2D (i.e., occlusal outline) plane, and this study predicted relief should be maintained, at least for a time. With the exception of *P. abelii* and *G. g. gorilla*, the prediction did not hold, as RFI decreased significantly in the other species (Table 2.15). In *P. abelii*, RFI was maintained (β = -8.642, p=0.869). The best-fit model for *G. g. gorilla* was the segmented regression, where β_1 decreased and then at a dental score of 0.72, β_2 was then maintained (Tables 2.15 and 2.20; Figures 2.4c). The segmented regression was the best fit for *P. pygmaeus* (Table 2.20); however, both β_1 and β_2 were negative and did not include 0 in the 95% C.I., indicating overall that RFI decreased (Table 2.15). Breakpoints were not estimated for *G. beringei*, *P. paniscus*, or *P. abelii*, and so, by default, linear regressions were determined to be the preferred model for these species. For both *P. t. troglodytes* and *P. t. schweinfurthii* the ΔAICc were > 2 (Table 2.20), but the βs estimated in the segmented regressions were not significantly

different from each other (Table 2.15); therefore, the linear regression models were preferred for these two species.

OPCRs

OPCRs represent the number of 'dental tools' available on the occlusal surface, and, like angularity, is also a measure of overall surface complexity. It was predicted that OPCRs should be maintained, at least for a proportion of dp_4 wear. The prediction held for all species, with the exception of *P. pygmaeus*, where OPCRs steadily declined (β = -28.045, p = 0.017) (Tables 2.12 and 2.21). The segmented regression was the best model only for *G. g. gorilla* (Table 2.21). In *G. g. gorilla*, OPCRs were maintained, there was a breakpoint at a relative age of 0.58, and then β_2 increased (Table 2.16; Figure 2.4d). Breakpoints were not estimated for *G. beringei* or *P. paniscus*, and so, by default, linear regressions were determined to be the preferred model for these two species. For both *P. t. troglodytes* and *P. pygmaeus*, the ΔAICc were < 2 (Table 2.21), and the βs estimated in the segmented regressions were not significantly different from each other (Table 2.16). Therefore, linear regression models were determined most appropriate for these two species.

PDE

PDE is a measure of tissue loss and it was predicted that as teeth wear, tissue loss should increase. With the exception of *P. abelii* and *P. t. schweinfurthii*, the prediction held; PDE increased significantly (+βs) in the other species. In *P. abelii*, PDE was maintained (β=21.36, p = 0.247). In *P. t. schweinfurthii*, β_1 increased, but β_2

was not different from 0 (Table 2.17) after the relative age of 0.71. For both *G. g. gorilla* and *P. pygmaeus*, the difference in ΔAICc values were < 2 (Table 2.22), and the βs estimated in the segmented regressions were not significantly different (Table 2.17). Therefore, linear regression models were determined most appropriate for these two species.

Associations Among Variables

Rank correlations (Tables 2.24- 2.30) revealed that nearly all the variables are highly correlated with each other within each species. OPCRs are consistently uncorrelated with the other variables, with the primary exceptions being in *G. beringei* and *P. pygmaeus*. In *G. beringei*, OPCRs are negatively associated with angularity (Table 2.24). In *P. pygmaeus*, OPCRs are positively associated with all other wear variables (Table 2.29).

Discussion

This study tested the hypothesis that, at least for a time, the occlusal topographic features on great ape dp_4s would be maintained. Tooth wear and tissue loss are inevitable, and so it was expected that slope, a measure of the overall occlusal gradient, and dentine exposure (a proxy for tissue loss) should show no evidence of maintenance. Given previous dental topographic analyses on primate molars, it was expected that measures of surface projection (i.e., relief) and overall occlusal topographic complexity would be maintained (i.e., angularity and OPCRs), at least for a proportion of the dp_4s' lifespan.

The results of this study revealed that OPCR, an assessment of occlusal complexity, was the only dental topographic variable to demonstrate a consistent

pattern of maintenance. With the exception of *P. pygmaeus*, maintenance of OPCRs was observed in all other species. This suggests that despite decreases or fluctuations in slope, angularity, RFI, and a steady loss of dental tissue, African great ape dp_4s, and possibly *P. abelii* dp_4s, wear in a manner that maintains the availability of 'dental tools.' Although the sample size for *P. abelii* is limited and only represents ~10% of the overall dental developmental schedule for that species, OPCRs were maintained. In contrast, OPCRs declined in *P. pygmaeus*. Orangutan deciduous premolars and molars possess crenulations, a distinct wrinkling pattern that increases the number of ridges and furrows (e.g., Swindler, 2002; Ankel-Simons, 2007), which initially produce high OPCR values. As orangutan postcanine teeth wear, the crenulations are removed leaving a smooth occlusal surface, which would decrease the OPCRs values. However, the crenulations cannot fully explain the overall dp_4 wear pattern observed in *P. pygmaeus*. The other species showed evidence of maintenance for at least one variable, but *P. pygmaeus* was the only species that lacked evidence of maintenance for any of the wear variables. A shift in wear (i.e., breakpoint) was observed in *P. pygmaeus* at a very early relative age when RFI dramatically decreased at ~51% of dental development. Although data are limited, orangutans tend to delay ingesting solids foods longer than the African apes (van Noordwijk et al., 2009; summarized in Table 3.1 in Chapter 3). The presence of this breakpoint may indicate a switch in feeding behavior and signal the commencement of infants starting to intake supplementary foods; however, data for this young age range are very limited and influenced by an individual with a very high RFI value (Figure 2.9c).

Within each species, rank correlation tests revealed that several of the wear variables were highly correlated, with the primary exception being OPCRs. In *G. beringei*, OPCRs were negatively correlated with angularity, the other measure of

complexity, and in *P. pygmaeus* OPCRs were positively associated with all other variables (Tables 2.24 and 2.29). Otherwise, for all other taxa, OPCRs were uncorrelated with any of the other measures of wear, suggesting that a change in the number of 'dental tools' is independent of changes in the other occlusal topographic measures (Winchester et al., 2014). Based on a maxillary molar sample from a wild population of *G. b. beringei*, Glowacka et al. (In Press) also report no significant correlations among dental topographic wear variables and OPCRs, suggesting that the distinction of OPCRs from other wear variables is not unique to great ape dp_4s. In the dp_4s of *P. pygmaeus*, it appears that OPCRs and the other variables are capturing the same wear signal, as demonstrated by the significant correlations and similar wear patterns. OPCRs were originally developed as a phylogenetic, scale-free method to segregate species into broad dietary categories (Evans et al. 2007); however, its application to wear studies is relatively recent (e.g., Glowacak et al., In Press). Further investigation is needed to untangle the interactions between OPCRs and other measures of occlusal topography (Chapter 3).

While future research is necessary, the dietary ecology of *P. pygmaeus* may help explain why its dp_4 wear pattern is distinct from the other great apes, and possibly, Sumatran orangutans (*P. abelii*). The dietary breadth of wild and rehabilitated orangutans is taxonomical diverse. The *Pongo spp.* diet includes multiple plant species, plant parts (e.g., fruit, seed, leaves, bark, pith), and, albeit very limited, animal protein (e.g., lorises, gibbons, tree rats, and fish) (Russon et al., 2008; Russon et al., 2009; Knott and Kahlenberg, 2011; Russon et al., 2014). Ecological studies have noted important differences between the habitats of *P. pygmaeus* (i.e., Bornean forests) and *P. abelii* (i.e., Sumatran forests). Dramatic fluctuations in the availability of fruit, the preferred food, are less likely to occur in Sumatran forests due to lower

densities of mast fruiting trees (i.e., dipterocarps) and higher densities of nutrient-rich volcanic soils (Marshal et al., 2009; Delgado and van Schaik, 2000). The variation in habitat probably explains why *P. pygmaeus* subsists on a greater proportion of fallback foods, which contain fewer nutrients and are more mechanically challenging to process, compared to foods consumed by *P. abelii* (Marshall and Wrangham, 2007; Vogel et al., 2008). Compared to the other great apes, *Pongo spp.* possess molars with thicker enamel, which is functionally advantageous for processing mechanically challenging foods (e.g., Molnar and Gnatt, 1977; Kay, 1981; Vogel et al., 2008), and there is no evidence for interspecific variation in the enamel thickness of molars between *P. pygmaeus* and *P. abelii* (Smith et al., 2012). Future work on orangutan dental ecology that merges research on how juveniles acquire ecological independence (e.g., Russon 2006) would shed greater light on orangutan dp_4 wear.

There was evidence of dental developmental factors explaining the observed presence of occlusal topographic maintenance for *G. g. gorilla* and *P. t. schweinfurthii*. In *G. g. gorilla*, the OPCRs were maintained but then increased when dental development was ~57% complete, indicating an increase in the availability of 'dental tools' on the dp_4s. The shift in wear pattern occurs just prior to the emergence of M_1 (i.e., ~60% of dental development; Tables 2.9 and 2.16). As the emergence of M_1 closely coincides with weaning in *G. g. gorilla*, this suggests a possible correspondence between an elevated intake of solid foods and an increase in dental tools available on the dp_4 (Kelley and Schwartz, 2010).

As indicated by the segmented regressions, occlusal maintenance of slope, angularity, and RFI were also observed in *G. g. gorilla*, at least for a proportion of dp_4 wear; however, for these wear variables the evidence for maintenance occurred at later relative ages. For slope, angularity, and RFI, the breakpoint occurred when

dental development was ~71-72% complete, which is shortly before the emergence of M_2 (i.e., dental development ~75% complete) (Table 2.9). Likewise, the segmented regression was the preferred model for slope, angularity, and PDE in *P. t. schweinfurthii*, and the breakpoints occurred at approximately the same relative age as gorillas (i.e., ~71-72% complete dental development), which also coincides with the emergence of M_2 in this species of chimpanzee (Table 2.10). The wear pattern for both *G. g. gorilla* and *P. t. schweinfurthii* was one where the occlusal topographic values declined but then maintained. The close alignment of the emergence of M_2 and the stasis of wear that followed highly suggests that the emergence of M_2 alleviated some of the chewing burden from the dp_4s in these two species of great apes.

Gorilla and *Pan* molars are generally characterized as having relatively thinner enamel when compared to *Pongo*; however, variation in the distribution of enamel may also relate to functional loads (e.g., Molnar and Gnatt, 1977; Macho and Spears, 1999; Schwartz, 2000; Smith et al., 2012; Skinner et al., 2015). Thinner enamel can be advantageous, as wear can remodel occlusal surfaces with thinner enamel more quickly than those with thicker enamel. Remodeling of the enamel via wear can generate accessory shearing crests, increasing the potential functional capacity for the occlusal surface (e.g., Rosenberger and Kinzey, 1976; Lucas, 2004; King et al., 2005). A preliminary observation of enamel thickness in three dp_4s representing *Pan*, *Gorilla*, and *Pongo* (Aiello et al., 1991) suggests that there is very little difference in enamel thickness; however, this remains to be tested. If dp_4 enamel thickness is comparable to values found in *G. g. gorilla* molars, then the observed increase of 'dental tools' on the dp_4s might be related to differences in enamel thickness or the distribution of the enamel throughout the dp_4 crown.

The pattern of dp_4 wear in *G. beringei* closely mirrored that of the maxillary

molars (Glowacka et al., In Press). Glowacka et al. (In Press) report that for a known-age population of wild mountain gorillas (*G. b. beringei*) slope, angularity, and RFI continual declined with age in all three maxillary molars. Even though the *G. beringei* sample in this study on dp_4s pooled unknown aged individuals from the subspecies *G. b. graueri* and *G. b. beringei*, a similar pattern was found for the *G. beringei* dp_4s—slope, angularity, and RFI steadily decreased with no evidence of maintenance or increase in occlusal topography. Interestingly, Glowacka et al. (In Press) report that for OPCRs only the M^1 s exhibited evidence of maintenance throughout wear, and OPCRs in M^2s and M^3s only declined over time. A similar trend as the M^1 s was observed for the dp_4s in this study—the OPCRs were maintained throughout wear. Interestingly, it appears that the dp_4 in *G. beringei* exhibits a similar wear pattern as the M^1 for the remaining dental topographic variables analyzed in this study. The comparisons between the dental arcades should be considered with caution; however, there is tentative evidence from a broad mammalian study that suggests the maxillary and mandibular molars wear in a similar manner. Evans and Jernvall (2009) report no differences in OPCRs between maxillary and mandibular molars.

Elgart (2010) and Galbany et al. (2016) report data for dentine exposure in African apes on dp_4s and molars, respectively. Given *G. beringei*'s mechanically challenging diet, it was expected that dentine exposure should be quite high in this species; however, both Elgart (2010) and Galbany et al. (2016) report evidence of low occlusal wear as indicated by dentine exposure. This study found a similar result. The maximum PDE value for *G. beringei* was only ~21%, the lowest maximum value compared to the other African apes, where values reached as high as ~55%.

Chimpanzees and bonobos prefer fruits, subsist on a broad, taxonomical diverse plant diet, and hunt for meat (Stump, 2011). Klukkert et al. (2012) reported no

significant differences in M_2 wear patterns for slope, angularity, or RFI in three subspecies of chimpanzees, two of which are considered in this study, *P. t. troglodytes* and *P. t. schweinfurthii*. As discussed above, there is evidence of dp_4 occlusal topographic maintenance in slope, angularity, OPCR, and PDE in *P. t. schweinfurthii*. In contrast, the only variable that showed evidence of maintenance in *P. t. troglodytes* was OPCRs. Hence, unlike the M_2s (Klukkert et al, 2012), this study did find subspecies wear pattern differences for the dp4s. Intriguingly, the overall dp_4 wear pattern for *P. t. troglodytes* was also the same wear pattern for bonobos (*P. paniscus*). Data on absolute ages for dental developmental in *P. paniscus* and *P. t. troglodytes* are lacking (reviewed in Chapter 3). The relative ages reported in this study found that in bonobos the M_2 emerges ~75% of dental development compared to *Pan t. schweinfurthii* and *P.t. troglodytes*, where the M_2 emerges ~70% of dental development (Table 2.10), suggesting that in *relative* terms M_2 emergence is slightly delayed in bonobos compared to chimpanzees. The relative delay of M_2 emergence may account for the observation that worn bonobo dp_4s had the lowest slope and RFI values among the great apes (Table 2.8). Among the available data for great apes, *P. paniscus'* diet also contains the highest phytolith load (Rabenold and Pearson, 2011). Perhaps, the relative delay of M_2 and the high phytolith content explains the dp_4 wear pattern. Relative age of M_2 emergence is the same for the two subspecies of chimpanzees and further work that tests differences in the proportion of phytoliths in the diet may shed light on why the dp_4 wear pattern differed in the chimpanzee subspecies.

A final point that needs consideration is whether signals of dp_4 occlusal maintenance are really due to dental senescence. Evidence of occlusal topographic maintenance is not necessarily equivalent to an optimum functional occlusal surface.

For example, there is evidence that some tooth wear is advantageous, as it increases the functional capacity of a tooth and can indirectly improve an animal's reproductive fitness (e.g., Gipps and Sanson 1984; Janis and Fortelius 1988; King et al., 2005; Veiberg et al. 2007). In contrast, evidence of topographic maintenance may signal the presence of an obliterated occlusal surface, which does not necessarily mean the complete loss of function. For example, there is evidence, particularly in lemurs, that heavily worn teeth 'work' for a time (e.g., Cuozzo and Sauthers, 2006). Still, evidence of occlusal topographic maintenance should signal that there is some preservation of the occlusal surface's functional ability. As defined by PDE, the most worn dp_4 in this sample of great apes belongs to *P.t. schweinfurthii*, and the PDE only comprises ~55% of the occlusal surface (Table 2.8). In terms of the other dental topographic values examined in this study, older individuals have signs of greater wear (i.e., lower values) than the youngest individuals, but the oldest individuals do not exhibit the most wear (i.e., the minimum values). As an example, Figure 2.10 is a montage of DEMs comparing the slope values among the youngest individuals, the oldest individuals, and the individuals with the lowest values of slope (i.e., the most wear as defined by slope). Figure 2.10 visually highlights that the oldest individuals do not have the most wear. In addition, in some taxa (e.g., *G. beringei* or *Pongo spp.*), even the most worn examples still exhibit a complex occlusal terrain, as these surfaces are not worn completely flat. Therefore, the evidence for occlusal topographic maintenance observed in this study is unlikely due to dp_4 dental senescence (Elgart, 2010).

Conclusion

Tooth wear is a function of age and older individuals tend to have more wear; however, the relationship between wear and age is not strictly linear, as wear rates can

change over time (e.g., Aiello et al., 1991; Elgart, 2010; Galbany et al., 2014; Galbany et al., 2016). In this respect, the great ape dp_4s are not different from molars, as older individuals tend to have more worn dp_4s, but not necessarily the *most* worn dp_4s. Similar to previously published data on great ape molars, intraspecific variations in the degree of dp4 wear are also present, as evidenced by the adjusted R^2 values. Among the best-fit models, relative age only explained up to ~60% of the variability. While this suggests that age is an important consideration in understanding dp_4 wear patterns, it is not the only predictor. The degree to which other socioecological factors (e.g., diet, teething, weaning) influence dp_4 wear patterns remains to be explored; however, there is evidence that dp_4 wear is not a reliable predictor for weaning in the great apes (Chapter 3). With the exception of *P. pygmaeus*, there is evidence of occlusal topographic maintenance for great ape dp_4s. Perhaps, in most of the great apes, the functional signal overshadows a potential weaning signal (Chapter 3). Another important age-related factor for some great apes species is the timing of molar emergence, particularly the M_2. The presence of the M_2 appears to alleviate some of the masticatory burden from the dp_4.

Further research on the biomechanics and structural properties of dp_4s would also be fruitful to understand dp_4 wear in general. For example, next to nothing is known about enamel thickness in great ape deciduous teeth, the distribution of enamel thickness, or other "stress shielding" (e.g., Chai et al., 2014) mechanisms, such as enamel prism decussation. A greater appreciation of the structural properties would assist in defining the functional capabilities and limitations of the great ape deciduous dentition, including the dp_4s, and help contextualize observed wear patterns on deciduous teeth.

References

Aiello, LC, Montgomery, C, Dean, MC. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397–412.

Altmann, SA. 1991. Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proc Natl Acad Sci USA 88:420–23.

Ankel-Simons, F. 2007. An introduction to primate anatomy. San Diego: Academic Press.

Atsushi, Y, Uasui, K, Sonomura, T., Iwai, H., Uemura, M. 2010. Development of deciduous and permanent dentitions in the upper jaw of the house shrew (*Suncus murinus*). Arch Oral Biol 55(4): 279–287.

Bartoń, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. https://CRAN.R-project.org/package=MuMIn

Baume, LJ. 1950. Physiological tooth migration and its significance for the development of occlusion: I. The biogenetic course of the deciduous dentition. J of Dent Res 29:123-132.

Bayne, K., Turner, PV. 2014. Animal environments and their impact on laboratory animal welfare. In: Bayne, K., Turner, PV. pp 77–94.

Birch, W., Dean, C. 2009. Rates of enamel formation in human deciduous teeth. Front Oral Biol 13:116-120.

Blanco, MB., Godfrey, LR. 2013. Does hibernation slow the ”pace of life in dwarf lemurs (*Cheirogaleus spp.*)? Int J Primatol 34:130-147

Borrero-Lopez, O, Pajares, A., Constantino, PJ, Lawn, BR. 2014. A model for predicting wear rates in tooth enamel. J Mech Behav Biomed Mater 37:226–34.

Boyer, DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol. 55 (6): 1118–37.

Bunn, JM, Ungar, PS. 2009. Dental topography and diets of four Old World monkey species. Am J Primatol 71(6): 466–77.

Burnham, KP., Anderson, DR. 2002. Model section and multimodel inferences: a practical information-theoretic approach (2 ed.). New York: Springer.

Catlett, KK., Schwartz, GT., Godfrey, LR. Jungers, WL 2010. “Life history space”: a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. Am J Phys Anthropol 142:391-404.

Chai, H, Lee, JJ, Constantino, PJ, Lucas, PW, Lawn, BR. 2009. Remarkable resilience of teeth. Proc Natl Acad Sci USA 106 (18): 7289–93.

Conolly, J., Lake, M. 2012. Geographical information systems in Archaeology. Cambridge: Cambridge University Press.

Cuozzo, FP., Sauther, ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. J Hum Evol. 51:490-505.

Cuozzo, FP., Ungar, PS. Sauther, ML. 2012. Primate dental ecology: How teeth respond to the environment. Am J Phys Anthropol 148:159-162.

Dale, P. 2005. Introduction to Mathematical Techniques used in GIS. Boca Raton: CRC Press.

Daniel, WW. 2000. Applied nonparametric statistics (2nd ed.). Pacific Grove, CA: Duxbury Thompson Learning.

Darnell, LA., Teaford, MF, Livi, KJT, Weihs, TP. 2010. Variations in the mechanical properties of *Alouatta palliata* molar enamel. Am J Phys Anthropol 141 (1): 7–15.

Dean, MC, Wood, BA. 1981. Developing pongid dentition and its use for aging individual crania in comparative cross-sectional growth studies. Folia Primatol 36 (1-2): 111–27.

Delgado, RA., van Schaik, CP. 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. Evol Anthropol 9:201-218.

Dennis, JC, Ungar, PS, Teaford, MF, Glander, KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125 (2): 152–61.

Elgart, AA. 2010. Dental wear, wear rate, and dental disease in the african apes. *Am* J of Primatol 71:1–11.

Evans, AR., Janis, CM. 2014. The evolution of high dental complexity in the horse lineage. Ann Zool Fennici 51:73-79.

Evans, AR., and Jernvall, J. 2009. Patterns and constraints in carnivoran and rodent dental complexity and tooth size. J Vert Paleo 29 24A.

Evans, AR, Wilson, GP, Fortelius, M, Jernvall, J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445: 78–81.

Evans, AR, Daly, ES, Catlett, KK, Paul, KS, King, SJ, Skinner, MM, Nesse, HP, Hublin, JJ, Townsend, GC, Schwartz, GT, Jernvall, J. 2016. A simple rule governs the evolution and development of hominin tooth size. Nature 530: 477-480.

Field, A. 2009. Discovering Statistics Using SPSS. Los Angeles: Sage.
Galbany, J, Altmann, J, Perez-Perez, A, Alberts, SC. 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. Am J Phys Anthropol 144 (1): 51–59.

Galbany, J., Imanizabayo, O., Romero, A., Vecellio, V., Glowacka, H., Cranfield, MR., Bromage, TG, Mudakikwa, A., Stoinski, TS, and McFarlin, S. 2016. Tooth wear and feeding ecology in mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol. Early View.

Galbany J, Romero A, Mayo-Alesón M, Itsoma F, Gamarra B, Pérez-Pérez A, Willaume E, Kappeler PM, Charpentier MJE. 2014. Age-related tooth wear differs between forest and savanna primates. PLoS One 9:e94938.

Gipps, JM, Sanson, GD. 1984. Mastication and digestion in *pseudocheirus*. In: Smith, AP and Hume, ID, editors. Possums and gliders. Sydney: Australian Mammal Society, p. 237–246.

Glowacka, H, McFarlin, S., Catlett, KK., Mudakikawa, A., Bromage, TG., Cranfiled, MR., Stoinksi, TS., Schwartz, GT. In Press.. Molar wear in wild population of known-age mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol.

Godfrey, LR, Samonds, KE, Jungers, WL, and Sutherland, MR. 2003. Dental development primate life histories. in primate life histories and socioecology In: Kappeler, PM and Pereira, ME, editors. Chicago: University of Chicago, pp. 177–203.

Godfrey, LR, Samonds , KE, Wright , PC, King, SJ. 2005. Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol (Basel). 76 2): 77–99.

Godfrey, LR., Schwartz, GT., Samonds, KE., Jungers, WL. Catlett, KK. 2006. The secrets of lemur teeth. Evol Anthropol 15:142-154.

GRASS Development Team, 2014. Geographic Resources Analysis Support System (GRASS) Software v. 7.0. Open Source Geospatial Foundation Project. http://grass.osgeo.org

Grine, FE. 2005. Enamel thickness of deciduous and permanent molars in modern *Homo sapiens.* Am J Phys Anthropol 126:14-31.

Hardin, AM, and Legge, SS. 2013. Geographic variation in nonmetric dental traits of the deciduous molars of *Pan* and *Gorilla*. Int J Primatol 34 (5): 1000–19.

Hillson, S. 2003. *Dental Anthropology*. Cambridge: Cambridge University Press.

Hillson, S. 2005. *Teeth*. Cambridge: Cambridge University Press.

Janis, CM, Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol Rev Camb Philos Soc 63 (2): 197–230.

Janson, CH., van Schaik, CP. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira, ME., Fairbanks, LA., editors. Juvenile Primates: Life history, development, and behavior. Chicago: University of Chicago Press. pp 57–74.

Järvinen, E, Valimaki, K, Pummila, M, Thesleff, I, Jernvall, J. 2008. The taming of the shrew milk teeth. *Evol Dev* 10 (4): 477–86.

Kavanagh, KD, Evans, AR, Jernvall, J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449 (7161): 427–32.

Kay, RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol.43 (2): 195–216.

Kay, RF. 1981. The nut-crackers: A new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141-151.

Kelley, J., Schwartz, G. T. 2010. Dental development and life history in living African and Asian apes. Proc Natl Acad Sci USA 107:1035-1040.

Kiliaridis, S. 2006. The importance of masticatory muscle function in dentofacial growth. Seminars in Orthodontics 12:110-119.

King, SJ, Arrigo-Nelson, SJ, Pochron, ST, Semprebon, GM, Godfrey , LR, Wright, PC, Jernvall, J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Aca Sci, USA 102 (46): 16579–83.

King, SJ. 2004. Relative timing of ontogenetic events in primates. J Zool 264 (3): 267–80.

Klukkert, ZS, Teaford, MF, Ungar, PS. 2012. A dental topographic analysis of chimpanzees. Am J Phys Anthropol .148 (2): 276-84.

Knott, CD, Kahlenberg, SM. 2011. Orangutans in perspective: understanding forced copulations. In Primates in Perspective, edited by C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, and R.M. Stumpf, 313–26. Oxford: Oxford University Press.

Kutner, MH., Nachtsheim, CJ., Neter, J. Li, W. 2005. Applied Linear Statistical Models. 5 edition. Boston: McGraw Hill.

Lucas, PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: CambridgeUniversity Press.

Lucas, PW, Corlett, RT, Luke, DA. 1986. Postcanine tooth size and diet in anthropoid primates. Zeitschrift fur Morphologies und Anthropologie 253–76.

Macena, MCB., Tornisiello Katz, CR., Heimer, MV., De Oliveira E Silva, JF. Costa, LB. 2011. Space changes after premature loss of deciduous molars among Brazilian children. Am J Orthod Dentofac 140:771-778.

Macchiarelli, R., Bondioli, L., Debenath, A., Mazurier, A., Tournepiche, J. F., Birch, W. Dean, MC.2006. How Neanderthal molar teeth grew. Nature 444:748-751.

Macho, GA., Spears, IR. 1999. Effects of loading on the biochemical behavior of molars of *Homo*, *Pan*, and *Pongo.* Am J Phys Anthropol 109:211-227.

Mahoney, P. 2013. Testing functional and morphological interpretations of enamel thickness along the deciduous tooth row in human children. Am J Phys Anthropol 151(4):518-25.

Marshall, AJ., Boyko, CM., Feilen, KL., Boyko, RH. Leighton, M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. Am J Phys Anthropol 140:603-614.

Matsuda, I., Tuuga, A., Hashimoto, C., Bernard, H., Yamagiwa, J., Fritz, J., Tsubokawa, K., Yayota, M., Murai, T., Iwata, Y., Clauss. 2014. Faecal particle size in free-ranging primates supports a 'rumination' strategy in the proboscis monkey (*Nasalis larvatus*). Oecologia 174:1127-1134.

Millette, JB., Sauther, ML., Cuozzo, FP. Ness, JL. 2012. The impact of dental impairment on ring-tailed lemur food processing performance. Am J Phys Anthropol 148:238-248.

Mahoney, P. 2015. Dental fast track: Prenatal enamel growth, incisor eruption, and weaning in human infants. Am J Phys Anthropol 156:407-421.

Marshall, AJ., Wrangham, RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219-1235.

McLeod, AI. 2011. Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2. https://CRAN.R-project.org/package=Kendall

Molnar, S., Gantt, DG. 1977. Functional implications of primate enamel thickness. Am J Phys Anthropol 46:447-454.

Muggeo, VM. 2003. Estimating regression models with unknown break-points. Statistics in Medicine 15:3055-3071.

Muggeo, VMR. 2008. Segmented: an R Package to fit regression models with broken-line relationships. R News, 8/1, 20-25. URL http://cran.r-project.org/doc/Rnews/.

Nanci, A. 2013. Ten Cate's Oral Histology: Development, structure, and function. St. Louis: Elsevier Mosby.

Osborn, HF. 1907. Evolution of Mammalian Molar Teeth: To and From the Triangular Type Including Collected and Revised Researches Trituberculy and New Sections on the Forms. (Biological Studies and Addresses. Vol. I). London:MacMillan.

Owen, R. 1840. Odontography; Or, a Treatise on the Comparative Anatomy of the Teeth; Their Physiological Relations, Mode of Development, and Microscopic Structure, in the Vertebrate Animals. By Richard Owen. Longon: Hippolyte Baillière.

Prinz, JF., Lucas, PW. 1995. Swallow thresholds in human mastication. Arch of Oral Biol 40:401-403.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rabenold, D, Pearson, OM. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. PLoS ONE 6 (12): e28379.

Rosenberger, AL, Kinzey, WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45 (2): 281–97.

Russon, AE. 2006. Acquisition of complex foraging skills in juvenile and adolescent orangutans (*Pongo pygmaeus*): Developmental influences. Aquatic Mammals 32:500-510.

Russon, AE., van Schaik, CP., Kuncoro, P., Ferisa, A., Hadayani, DP. van Noordwijk, MA. 2009. Innovation and intelligence in orangutans. In: Wich, SA., Utami, SS., Mitra Setia, T. van Schaik, C. editors. Orangutans: Geographic Variation in Behavioral Ecology and Conservation. Oxford: Oxford University Press. pp 279–298.

Russon, AE., Compost, A., Kuncoro, P. Ferisa, A. 2014. Orangutan fish eating, primate aquatic fauna eating, and their implications for the origins of ancestral hominin fish eating. J Hum Evol 50-63.

Segura, AM., Milessi, AC., Vögler, R., Galván-Magaña, F. Muggeo, V. 2013. The determination of maturity stages in male elasmobranchs (Chondrichthyes) using a segmented regression of clasper length on total length. Can J Fish Aquat Sci 70:830-833.

Schroer, K., Wood, B. 2015. Modeling the dental development of fossil hominins through the inhibitory cascade. J Anat 226:150-162.

Schwartz, GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221-244.

Schwartz, GT. 2012. Growth, development, and life history throughout the evolution of *Homo.* Curr Anthrolpol 53:S395-S408.

Schwartz, GT, Samonds, KE, Godfrey, LR, Jungers, WL, Simons, EL. 2002. Dental microstructure and life history in subfossil malagasy lemurs. Pro Natl Acad Sci, USA 99(9): 6124–29.

Simpson, GG. 1936. Studies on the earliest mammalian dentition. Dental Cosmos 78:791–800.

Matthew, MS., Zeresenay, A., Charleen, G. Jean-Jacques, H. 2015. Enamel thickness trends in Plio-Pleistocene hominin mandibular molars. J Hum Evol 85:35-45.

Smith, BH, Crummett, TL Brandt, KL. 1994. Ages of eruption of primate teeth: acompendium for aging individuals and comparing life histories. Yrbk Phys Anthropol 37 177–231.

Smith, TM., Kupczik, K., Machanda, Z., Skinner, M. M. Zermeno, J. P. 2012. Enamel thickness in Bornean and Sumatran orangutan dentitions. Am J Phys Anthropol 147:417-426.

Sokal, RR., Rohlf, JF. 1994. Biometry: The Principles and Practices of Statistics in Biological Research. 3rd ed. New York: W.H. Freeman and Co.

Stroik, L. 2014. The dietary competitive environment of the origination and early diversification of Euprimates in North America. PhD Dissertation. Arizona State University.

Stumpf, R. 2011. Chimpanzees and bonobos: Inter- and Intraspecies Diversity. In: Campbell, C.J., Fuentes, A., Mackinnon, KC., Bearder, SK. Stumpf, RM. editors. Primates in Perspective. Oxford: Oxford University Press. pp 340–356.

Swindler, DR. 2002. Primate dentition: An introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

Teaford, MF. 2000. Primate dental functional morphology revisited. Development, function and evolution of teeth Cambridge: Cambridge University Press p 290-304.

Tanaka, EM., Sato, S. 2008. Longitudinal alteration of the occlusal plane and development of different dentoskeletal frames during growth. Am J Orthod Dentofac 134:602.e1-602.e11.

Ungar, PS, Williamson, M. 2000. Exploring the effects of tooth wear on functionalmorphology: a preliminary study using dental topographic analysis. http://palaeo-electronica.org/2000_1/gorilla/issue1_00.htm.1(18):1–18.

Ungar, PS. 2007. Dental topography and human evolution. In: Bailey, SE., Hublin, JJ., editors. Dental perspectives on human evolution: state of the art research in dental paleoanthropology. Dordrechet: Springer. p 321–344.

Ungar, PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46 (5): 605–22.

Ungar, PS. 2010. Mammal teeth: origin, evolution, and diversity. Baltimore: The John Hopkins University Press.

Ungar, PS, M'Kirera, F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proc Natl Acad Sci, USA* 100 (7): 3874–77.

van Noordwijk, MA., Sauren, SEB., Nuzuar, AA., Morrogh-Bernard, HC., Utami Atmoko, SS. van Schaik, CP. 2009. Development of independence. In: Wich, SA., Utami, SS., Mitra Setia, T. van Schaik, C. editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 189–204.

Veiberg, V, A Mysterud, E Bjorkvoll, R Langvatn, LE Loe, RJ Irvine, C Bonenfant, F., Couweleers, and NC Stenseth. 2007. Evidence for a trade-off between early growth and tooth wear in Svalbard reindeer. J Anim Ecol 76 (6): 1139–48.

Venkataraman, VV, Glowacka, H, Fritz, J, Clauss, M, Seyoum, C, Nguyen, N, Fashing, PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155 (1): 17–32.

Vogel, ER., van, W., JT, Lucas, PW., Atmoko, SSU., van, S., CP, Dominy, NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii.* J Hum Evol 55:60-74.

Wheatley, D., Gillings, M. 2002. Spatial technology and archaeology: The archaeological applications of GIS. Boca Raton: Taylor and Francis.

Wickham, H. 2009. Ggplot2: elegant graphics for data analysis. New York: Springer.

Winchester, JM, Boyer, DM, St. Clair, EM, Gosselin-Ildari, AD, Cooke, SB, Ledogar, JA. 2014. Dental topography of platyrrhines and prosimians: convergence and contrasts. Am J Phys Anthropol 153:29-44.

Zuccotti, LF, MD Williamson, WF Limp, and PS Ungar. 1998. Technical note: modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107 (1): 137–42.

Table 2.1. Sample sizes, relative age ranges, and taxa

Taxon	Sample Size	Relative Age Ranges
Gorilla beringei	18*	0.519- 0.846
Gorilla gorilla gorilla	85	0.539- 0.952
Pan paniscus	29	0.519- 0.793
Pan troglodytes schweinfurthii	43	0.539- 0.793
Pan troglodytes troglodytes	53	0.539- 0.832
Pongo pygmaeus	41**	0.481- 0.861
Pongo abelii	9**	0.609- 0.712
	N=278	**0.481-0.952**

*Three individuals are *Gorilla beringei beringei* and the remaining individuals belong to the subspecies *Gorilla beringei graueri*. For the purposes of this study, gorilla subspecies were pooled. **Three of the specimens (a single *Pongo abelii* individual and two *Pongo pygmaeus* individuals were captive; however, since these individuals were very young they were kept in the final sample as they represented individuals with no occlusal wear).

Table 2.2. Dental developmental scoring system used to assign proxy ages (modified from King, 2004)

Score	Developmental state of deciduous tooth	Developmental state of molar or succedaneous tooth
1	Tooth not visible	Tooth not visible
2	Visible in crypt	Visible in crypt
3	Piercing or emerging above alveolar bone	Piercing or emerging above alveolar bone
4*	Shed	NA
4	Fully emerged to occlusal plane	Fully emerged to occlusal plane

* Individuals were assumed to have normal dental development. In individuals with emerging or fully erupted permanent dentition, the deciduous teeth that likely preceded it was considered shed and scored a 4 (see text for additional details).

Table 2.3. Interpretations for β modeling slope, angularity, RFI, OPCR, and PDE wear*

Statistically significant β	Conclusion
Greater than 0 (i.e., positive)	Suggests **increase** in occlusal topographic features
Not different from 0	Suggests **maintenance** of occlusal topographic features
Less than 0 (i.e., negative)	Suggests **decrease** of occlusal topographic features

* For PDE, it is expected that a linear model with a positive slope will be the best model, as tissue loss should steadily increase throughout wear.

Table 2.4. Interpretations for β based on King et al.(2005) conclusions and data set

Statistically significant β	Conclusion
Relative Crown Relief	Less than 0 (i.e., negative). Suggests **decrease** of occlusal topographic features, then **maintenance** of occlusal topographic features (i.e., not different from 0).
2D Relative Shearing Blade Length	Greater than 0 (i.e., positive). Suggests **increase** in occlusal topographic features then **decrease** of occlusal topographic features (i.e., slope less than 0).
3D Relative Shearing Blade Length	**Maintenance** of occlusal topographic features (i.e., not different from 0) followed by a **decrease** (i.e., less than 0.).

Table 2.5. Results of linear regressions using King et al., (2005) data set

Variable	*B* (SE)	Adjusted R^2
Relative Crown Relief	**-0.0143 (0.002) *****	**0.542*****
2D Relative Shearing Blade Length	0.010 (0.005)	0.0407
3D Relative Shearing Blade Length	**-0.036 (0.006)*****	**0.403*****

$^*p \leq 0.05$ $^{**}p \leq 0.01$ $^{***}p \leq 0.001$

Table 2.6. Results of segmented regressions using King et al., (2005) data set

Variable	Range	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
Relative Crown Relief	1.29-1.76	-0.038 (-0.0504, -0.0248)	-0.002 (-0.0069, 0.0035)	<0.0001***	8.41 (1.05)	51	0.738
2D Relative Shearing Blade Length	1.55-2.61	0.046 (0.032, 0.059)	-0.052 (-0.0778, -0.026)	<0.0001***	13.05 (1.20)	51	0.545
3D Relative Shearing Blade Length	2.04-3.82	-0.008 (-0.026, 0.010)	-0.087 (-0.124, -0.051)	0.0012**	13.40 (2.05)	51	0.549

$^*p \leq 0.05$ $^{**}p \leq 0.01$ $^{***}p \leq 0.001$ 95% C.I. lower, upper BK = Estimated Ages

Table 2.7. King et al. (2005) model comparison results

Variable	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
Relative Crown Relief	-114.556	~0.0000	-142.582	0.9999	28.026	Segmented
2D Relative Shearing Blade Length	5.722	~0.0000	-32.635	~1.0000	38.4205	Segmented
3D Relative Shearing Blade Length	18.220	0.0017	5.466	0.9983	12.754	Segmented

*Table 2.8. Descriptive Statistics**

	Slope	Angularity	RFI	OPCRs	PDE
G. beringei	49.76 - 33.97	88.11 - 86.36	194.2 - 141.7	65.25 - 51.50	0.00 - 21.12
G. g. gorilla	48.75 - 27.62	88.14 - 83.65	179.0 - 130.3	68.62 - 40.12	0.00 - 51.42
P. paniscus	47.02 - 22.72	88.63 - 84.33	172.8 - 124.0	68.00 - 43.50	0.00 - 45.74
P. t. schweinfurthii	44.40 - 23.40	88.39 - 84.23	169.5 - 132.1	65.88 - 43.38	0.00 - 54.71
P. t. troglodytes	43.20 - 25.47	88.42 - 83.43	166.1 - 125.5	74.25 - 40.62	0.00 - 44.82
P. pygmaeus	42.64 - 28.06	88.62 - 85.35	168.8 - 127.5	75.38 - 47.12	0.00 - 20.14
P. abelii	34.94 - 27.82	87.77 - 86.41	148.1 - 131.6	59.12 - 48.25	0.54 - 6.74

* Ranges are reported from maximum to minimum because maximum values represent individuals with little to no wear and the youngest individuals (i.e., lowest dental scores). The minimum values correspond to individuals with the most wear for those measures, but the minimum values do not necessarily represent the oldest individuals (i.e., highest dental scores). Means or medians are not reported because each taxon represents a variety of ages and wear states.

Table 2.9. Mean relative ages for each state of Gorilla *mandibular molar development*. Scores are reported as percentages and are interpreted as what proportion of the normal, expected dental development is complete. *

		G. beringei Mean (Median)	***G. g. gorilla*** Mean (Median)
M_1	Not Visible	n/a	n/a
	Visible	54.8 (54.3) (n=3)	57.0 (57.1) (n=16)
	Emerging	**59.0 (59.0) (n=5)**	**59.5 (59.6) (n=22)**
	Complete	68.4 (60.8) (n=10)	69.5 (65.3) (n=47)
M_2	Not Visible	53.1 (53.1) (n=2)	56.5 (55.8) (n=10)
	Visible	60.1 (59.7) (n=11)	61.35 (60.6) (n=57)
	Emerging	**70.7 (69.7) (n=3)**	**75.7 (74.5) (n=9)**
	Complete	81.7 (81.7) (n=2)	82.5 (83.2) (n=9)
M_3	Not Visible	60.5 (59.5) (n=14)	61.5 (60.1) (n=64)
	Visible	74.2 (72.8)(n=4)	72.0 (68.6) (n=19)
	Emerging	**n/a**	**90.4 (90.4) (n=2)**
	Complete	n/a	n/a

*Note: The entire sample is reported for *each* stage of molar development. For example, there are 18 *G. beringei* specimens. The same 18 individuals are represented for each molar position.

Table 2.10. Mean relative ages for each state of mandibular molar development in Pan. Scores are reported as percentages and are interpreted as what proportion of the normal, expected dental development is complete.*

		P. paniscus Mean (Median)	***P.t. schweinfurthii*** Mean (Median)	***P.t. troglodytes*** Mean (Median)
M_1	Not Visible	n/a	n/a	n/a
	Visible	56.1 (56.6) (n=9)	56.3 (56.7) (n=14)	56.1 (56.7) (n=9)
	Emerging	**62.3 (61.5) (n=4)**	**59.4 (59.1) (n=7)**	**57.5 (57.5) (n=2)**
	Complete	65.5 (63.5) (n=16)	67.1(65.4) (n=22)	68.6 (66.6) (n=42)
M_2	Not Visible	55.8 (56.4) (n=6)	55.2 (55.4) (n=9)	54.9 (54.2) (n=6)
	Visible	61.6 (61.6) (n=19)	62.0 (62.2) (n=27)	63.5 (63.6) (n=24)
	Emerging	**74.6 (74.6) (n=4)**	**70.4 (69.2) (n=3)**	**69.1 (68.3) (n=17)**
	Complete	n/a	74.4 (73.8) (n=4)	78.9 (79.3) (6)
M_3	Not Visible	61.1 (60.9) (n=26)	60.8 (60.4) (n=37)	62.7 (62.9) (n=30)
	Visible	71.5 (71.2) (n=3)	71.6 (70.2) (n=6)	70.4 (68.3) (n=23)
	Emerging	**n/a**	**n/a**	**n/a**
	Complete	n/a	n/a	n/a

*Note: The entire sample is reported for *each* stage of molar development. For example, there are 29 *P. paniscus* specimens. The same 29 individuals are represented for each molar position.

Table 2.11. Mean relative ages for each state of mandibular molar development for Pongo. Scores are reported as percentages and are interpreted as what proportion of the normal, expected dental development is complete. *

		P. pygmaeus Mean (Median)	***P. abelii*** Mean (Median)
M_1	Not Visible	n/a	n/a
	Visible	55.4 (56.7) (n=14)	n/a
	Emerging	**57.7 (58.7) (n=3)**	**60.6 (60.6) (n=1)**
	Complete	69.9 (69.2) (n=24)	64.9 (63.5) (n=8)
M_2	Not Visible	53.4 (53.9) (n=7)	n/a
	Visible	60.9 (60.1) (n=20)	62.6 (62.0)(n=7)
	Emerging	**70.5 (69.2) (n=6)**	**70.7 (70.7)(n=2)**
	Complete	76.4 (75.5) (n=8)	n/a
M_3	Not Visible	60.3 (58.4) (n=28)	62.2 (61.8) (n=6)
	Visible	72.2 (70.2) (n=13)	68.2 (70.2) (n=3)
	Emerging	**n/a**	**n/a**
	Complete	n/a	n/a

*Note: The entire sample is reported for *each* stage of molar development. For example, there are 41 *P. pygmaeus* specimens. The same 41 individuals are represented for each molar position.

Table 2.12. Summary of simple linear regression results

Species	Slope		Angularity		RFI		OPCRs		PDE	
	B (SE)	Adjusted R^2	*B* (SE)	Adjusted R^2	*B* (SE)	Adjusted R^2	*B* (SE)	Adjusted R^2	*B* (SE)	Adjusted R^2
G. beringei	-42.48 (8.32) ***	0.596 ***	-3.8719 (0.96) ***	0.4754 ***	-123.73 (29.95) ***	0.4859 ***	21.212 (10.651) (n.s)	0.1486 (n.s)	58.439 (11.468) ***	0.5949 ***
G. g. gorilla	-38.076 (4.477) ***	0.4592 ***	-5.5779 (0.7797) ***	0.374 ***	-68.042 (12.56) ***	0.2524 ***	11.351 (7.068) (n.s)	0.112 (n.s.)	88.141 7.227 ***	0.6374
P. paniscus	-62.406 (13.083) ***	0.4372 ***	-9.083 (2.473) **	0.3084 **	-117.70 (28.09) ***	0.3716 ***	-22.231 (15.983) (n.s)	0.0323 (n.s.)	125.59 (42.33) **	0.2242 **
P. t. schweinfurthii	-48.834 (9.661) ***	0.3689 ***	-6.596 (1.626) ***	0.269 ***	-80.21 (20.11) ***	0.262 ***	11.135 (12.822) (n.s)	-0.0059 (n.s.)	111.58 (33.52) **	0.1935 **
P. t. troglodytes	-50.76 (5.87) ***	0.5866 ***	-8.7982 (1.1395) ***	0.5299 ***	-89.45 (12.70) ***	0.4831 ***	9.052 (12.304) (n.s)	-0.0089 (n.s.)	114.27 (17.73)	0.4382 ***
Pongo abelii	-3.075 (21.182) n.s.	-0.1394 (n.s.)	-0.843 (3.810) n.s.	-0.1349 n.s.	-8.462 (49.541) n.s.	-0.1381 n.s.	-50.84 (25.74) n.s.	0.2661 n.s.	21.36 (16.92) n.s.	0.06907 n.s.
P. pygmaeus	-25.446 (4.222) ***	0.4689 ***	-4.9444 (0.9927) ***	0.3731 ***	-42.363 (10.772) ***	0.2656 ***	-28.045 (11.230) *	0.1158 *	42.316 (5.949) ***	0.5598 ***

n.s = not significant *$p \leq 0.05$ **$p \leq 0.01$ ***$p \leq 0.001$

Table 2.13. Summary of segmented regressions for slope

Species	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
G. beringei	-63.28 -103.1, -23.46)	-12.92 -114.6, 88.75)	0.750	0.701 (0.105)	14	0.592
G. g. gorilla	-69.36 (-93.34, -45.37)	3.07 (-23.77, 29.91)	0.002**	0.716 (0.027)	81	0.5382
P. paniscus	No breakpoints estimated.					
P. t. schweinfurthii	-72.33 -97.81, -46.85)	56.12 (-69.73, 182.00)	0.03912*	0.707 (0.030)	39	0.4586
P. t. troglodytes	-76.78 (-146.30, -7.30)	-41.88 -58.57, -25.20)	0.4074	0.625 (0.065)	49	0.5909
P. abelii	-66.32 (-566.7, 434.1)	26.92 (-100.7, 154.5)	0.9607	0.642 (0.062)	5	-0.4363
P. pygmaeus	-34.30 (-49.00, -19.59)	3.19 (-37.29, 43.67)	0.2494	0.723 (0.044)	37	0.4922

*$p \leq 0.05$ **$p \leq 0.01$ ***$p \leq 0.001$ 95% C.I. lower, upper BK = dental scores

Table 2.14. Summary of segmented regressions for angularity

Species	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
G. beringei	-5.487 (-10.110, -0.866)	1.406 (-10.40, 13.210)	0.8182	0.746 (0.069)	14	0.4591
G. g. gorilla	-10.22 (-14.520, -5.908)	0.2175 (-4.603, 5.038)	0.01742*	0.713 (0.033)	81	0.4314
P. paniscus	-12.310 (-26.83, 2.219)	-7.301 (-17.03, 2.424)	0.2922	0.619 (0.100)	25	0.2635
P. t. schweinfurthii	-10.82 (-15.03, -6.523)	13.38 (-7.364, 34.130)	0.0192*	0.709 (0.026)	39	0.3982
P. t. troglodytes	-5.864 (-9.933, -1.796)	-15.88 (-25.08, -6.684)	0.1765	0.713 (0.034)	49	0.5541
P. abelii	-28.69 (-95.740, 38.35)	11.01 (-6.087, 28.11)	0.2216	0.640 (0.018)	5	0.2063
P. pygmaeus	No breakpoints estimated.					

*$p \leq 0.05$ **$p \leq 0.01$***$p \leq 0.001$ 95% C.I. lower, upper BK = dental scores

Table 2.15. Summary of segmented regressions for RFI

Species	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
G. beringei			No breakpoints estimated.			
G. g. gorilla	-170.80 (-235.6, -106.1)	67.64 (-4.637, 140.2)	<0.0001***	0.716 (0.022)	81	0.4092
P. paniscus			No breakpoints estimated.			
P. t. schweinfurthii	-127.60 (-194.3, -61.91)	42.36 (-122.3, 208.80)	0.1652	0.683 (0.034)	39	0.3083
P. t. troglodytes	-188.60 (-375.8, -1.305)	-68.04 (-103.1, -32.93)	0.2141	0.605 (0.039)	49	0.5005
P. abelii			No breakpoints estimated.			
P. pygmaeus	-883.90 (-1708.00, 59.680)	-30.76 (-51.69, -9.837)	0.0064**	0.505 (0.008)	37	0.4211

*$p \leq 0.05$ **$p \leq 0.01$ ***$p \leq 0.001$ 95% C.I. lower, upper BK = dental scores

Table 2.16. Summary of segmented regressions for OPCRs

Species	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
G. beringei			No breakpoints estimated.			
G. g. gorilla	-244.1 (-559.50, 71.26)	18.2 (3.689, 32.71)	0.03352*	0.575 (0.014)	81	0.09002
P. paniscus			No breakpoints estimated.			
P. t. schweinfurthii	1.00 (-33.99, 35.99)	67.06 (-350.00, 484.20)	0.8481	0.717 (0.182)	39	-0.03536
P. t. troglodytes	-260.40 (-1274.00, 753.00)	24.19 (-4.338, 52.71)	0.2168	0.567 (0.045)	49	0.03395
P abelii	-415.10 (-1333.0, 503.10)	-28.11 (-133.2, 77.03)	0.716	0.618 (0.009)	5	0.2089
P. pygmaeus	-41.86 (-72.51, -11.21)	119.50 (-75.29, 314.30)	<0.9999	0.775 (0.030)	37	0.1529

*$p \leq 0.05$ **$p \leq 0.01$ ***$p \leq 0.001$ 95% C.I. lower, upper BK = dental scores

Table 2.17. Summary of segmented regressions for PDE

Species	β_1 (95% C.I.)	β_2 (95% C.I.)	Davies Test *p*-value	BKs (SE)	df	Adjusted R^2
G. beringei	97.180 (31.29, 163.10)	6.593 (-70.39, 83.58)	0.4059	0.697 (0.052)	14	0.6333
G. g. gorilla	77.52 (54.79, 00.3)	152.40 (58.50, 246.3)	0.2741	0.802 (0.048)	81	0.6416
P. paniscus	205.6 (57.22, 353.9)	-119.9 (-658.20, 418.3)	0.3386	0.696 (0.051)	24	0.2393
P. t. schweinfurthii	196.9 (115.0, 278.8)	-333.5 (-1310, 642.8)	0.01983*	0.714 (0.056)	39	0.3348
P. t. troglodytes	92.03 (34.28, 149.8)	179.90 (-16.28, 376.1)	0.7622	0.721 (0.076)	49	0.4301
P. abelii	96.28 (25.02, 167.5)	-53.09 (-555.60, 449.4)	0.1232	0.657 (0.065)	5	0.5363
P. pygmaeus	14.26 (-20.28, 48.81)	73.34 (40.69, 106.00)	0.08153	0.667 (0.038)	36	0.606

*$p \leq 0.05$ **$p \leq 0.01$ ***$p \leq 0.001$ 95% C.I. lower, upper BK = dental scores

Table 2.18. AICcs results for slope

Species	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
G. beringei	95.49765	0.926	100.55266	0.0740	5.05501	Linear
G. g. gorilla	459.4551	0.0043	448.5598	0.9957	10.8953	Segmented
P. paniscus			n/a			Linear
P. t. schweinfurthii	244.5618	0.1338	240.8274	0.8661	3.7344	Segmented
P. t. troglodytes	274.1718	0.7426	276.2908	0.2574	2.119	Linear
P. abelii	49.5173	0.9999	67.7723	0.0001	18.2556	Linear
P. pygmaeus	194.1709	0.6301	195.2361	0.3699	1.0652	Linear*

*See text for details

Table 2.19. AICcs results for angularity

Species	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
G. beringei	17.592	0.938	23.0238	0.0620	5.432	Linear
G. g. gorilla	162.388	0.0541	156.666	0.9456	5.722	Segmented
P. paniscus	76.6499	0.9322	81.8908	0.0678	269.389	Linear
P. t. schweinfurthii	91.3146	0.0596	85.8066	0.9407	5.50796	Segmented
P. t. troglodytes	100.4149	0.4830	100.2786	0.5170	0.1363	Linear*
P. abelii	18.6382	0.9985	31.5919	0.0015	12.9537	Linear
P. pygmaeus			n/a			Linear

*See text for details

Table 2.20. AICcs results for RFI

Species	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
G. beringei			n/a			Linear
G. g. gorilla	634.8257	0.0002	617.2938	0.9998	17.5319	Segmented
P. paniscus			n/a			Linear
P. t. schweinfurthii	307.6163	0.5088	307.6867	0.4912	0.0701	Linear*
P. t. troglodytes	355.9920	0.6051	356.8453	0.3949	0.8533	Linear*
P. abelii			n/a			Linear
P. pygmaeus	270.9676	0.0316	265.1206	0.9684	6.847	Segmented

*See text for details.

Table 2.21. AICcs results for OPCRs

Species	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
G. beringei			n/a			Linear
G. g. gorilla	537.2112	0.1176	533.1817	0.8823	4.0295	Segmented
P. paniscus			n/a			Linear
P. t. schweinfurthii	268.9066	0.8858	273.0041	0.1142	4.0975	Linear
P. t. troglodytes	352.6299	0.5436	352. 9962	0.4543	0.3663	Linear*
P. abelii	53.02441	0.9998	69.8617	0.0002	16.847	Linear
P. pygmaeus	274.3795	0.6398	275.5282	0.3602	1.1487	Linear*

*See text for details.

Table 2.22. AICcs for PDE

Species	Linear AICc	ω Linear AICc	Segmented AICc	ω Segmented AICc	|ΔAICc|	Preferred Model
G. beringei	107.0373	0.8241	110.1256	0.1759	3.0883	Linear
G. g. gorilla	541.0413	0.6697	542.4546	0.3303	1.4133	Linear*
P. paniscus	233.1823	0.8128	236.1193	0.1872	2.937	Linear
P. t. schweinfurthii	351.5614	0.0623	346.1393	0.9377	5.4221	Segmented
P. t. troglodytes	391.3267	0.8474	394.7552	0.1522	3.4702	Linear
P. abelii	45.4722	0.9929	55. 3709	0.0071	9.8987	Linear
P. pygmaeus	216.8126	0.3216	215.3198	0.6784	1.4928	Linear*

*See text for details.

Table 2.23. Best-fit models and interpretations for occlusal topographic variables

Species	Slope	Angularity	RFI	OPCRs	PDE
G. beringei	(Linear) Decrease	(Linear) Decrease	(Linear) Decrease	(Linear) Maintenance	(Linear) Increase
G. g. gorilla	(Segmented) Decrease then Maintenance	(Segmented) Decrease then Maintenance	(Segmented) Decrease then Maintenance	(Segmented) Maintenance then Increase	(Linear) Increase
P. paniscus	(Linear) Decrease	(Linear) Decrease	(Linear) Decrease	(Linear) Maintenance	(Linear) Increase
P. t. schweinfurthii	(Segmented) Decrease then Maintenance	(Segmented) Decrease then Maintenance	(Linear) Decrease	(Linear) Maintenance	(Segmented) Increase then Maintenance
P. t. troglodytes	(Linear) Decrease	(Linear) Decrease	(Linear) Decrease	(Linear) Maintenance	(Linear) Increase
P. abelii	(Linear) Maintenance	(Linear) Maintenance	(Linear) Maintenance	(Linear) Maintenance	(Linear) Maintenance
P. pygmaeus	(Linear) Decrease	(Linear) Decrease	(Segmented) Decrease	(Linear) Decrease	(Linear) Increase

Table 2.24. Rank correlations for Gorilla beringei *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	**Angularity**	**Relief Index**	**OPCRs**	**PDE**
Slope	--				
Angularity	**0.451 (0.009)****	--			
Relief Index	**0.787 (<0.0001)****	**0.472 (0.006)****	--		
OPCRs	-0.139 (0.425)	**-0.351 (0.044)***	-0.173 (0.323)	--	
PDE	**-0.812 (<0.0001)****	**-0.468 (0.009)****	**-0.697 (<0.0001)****	0.230 (0.200)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.25. Rank correlations for Gorilla gorilla gorilla *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	**Angularity**	**Relief Index**	**OPCRs**	**PDE**
Slope	--				
Angularity	**0.616 (<0.0001)****	--			
Relief Index	**0.766 (<0.0001)****	**0.585 (<0.0001)****	--		
OPCRs	-0.063 (0.397)	-0.009 (0.906)	-0.050 (0.497)	--	
PDE	**-0.535 (<0.0001)****	**-0.507) (<0.0001)****	**-0.449 (<0.0001)****	0.072 (0.332)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.26. Rank correlations for Pan troglodytes troglodytes *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	Angularity	Relief Index	OPCRs	PDE
Slope	--				
Angularity	**0.666 (<0.0001)****	--			
Relief Index	**0.837 (<0.0001)****	**0.588 (<0.0001)****	--		
OPCRs	0.039 (0.684)	0.030 (0.753)	0.090 (0.345)	--	
PDE	**-0.477 (<0.0001)****	**-0.417 (<0.0001)****	**-0.401 (<0.0001)****	0.066 (0.490)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.27. Rank correlations for Pan troglodytes schweinfurthii *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	Angularity	Relief Index	OPCRs	PDE
Slope	--				
Angularity	**0.639 (<0.0001)****	--			
Relief Index	**0.748 (<0.0001)****	**0.511 (<0.0001)****	--		
OPCRs	0.023 (0.826)	0.094 (0.374)	0.068 (0.523)	--	
PDE	**-0.460 (<0.0001)****	**-0.440 (<0.0001)****	**-0.324 (0.003)****	-0.019 (0.858)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.28. Rank correlations for Pan paniscus *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	Angularity	Relief Index	OPCRs	PDE
Slope	-				
Angularity	**0.605 (<0.0001)****	--			
Relief Index	**0.816 (<0.0001)****	**0.531 (<0.0001)****	--		
OPCRs	0.106 (0.412)	0.161 (0.212)	0.097 (0.454)	--	
PDE	**-0.594 (<0.0001)****	**-0.496 (<0.001)****	**-0.501 (<0.0001)****	-0.099 (0.435)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.29. Rank correlations for Pongo pygmaeus *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	Angularity	Relief Index	OPCRs	PDE
Slope	--				
Angularity	**0.656 (<0.0001)****	--			
Relief Index	**0.729 (<0.0001)****	**0.463 (<0.0001)****	--		
OPCRs	**0.390 (<0.0001)****	**0.466(<0.0001)****	**0.314 (0.004)****	--	
PDE	**-0.578 (<0.0001)****	**-0.585 (<0.0001)****	**-0.415 (<0.0001)****	**-0.390 (0.001)****	--

** p-value ≤ 0.01 *p-value ≤ 0.05

Table 2.30. Rank correlations for Pongo abelii *(Kendall's tau method)* (P-values are in parentheses.)

	Slope	**Angularity**	**Relief Index**	**OPCRs**	**PDE**
Slope	--				
Angularity	0.500 (0.061)	--			
Relief Index	**0.667 (0.012)***	0.278 (0.297)	--		
OPCRs	0.366 (0.173)	0.423 (0.116)	0.310 (0.249)	--	
PDE	-0.167 (0.532)	-0.333 (0.211)	-0.056 (0.835)	-0.141 (0.600)	--

** p-value ≤ 0.01 *p-value ≤ 0.05

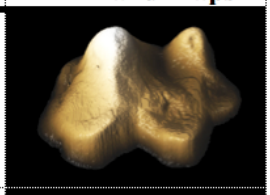
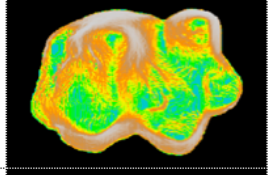
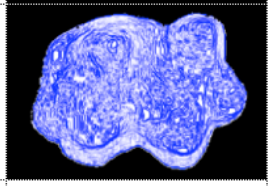
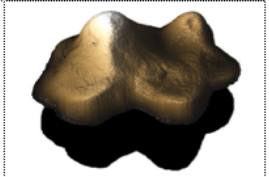
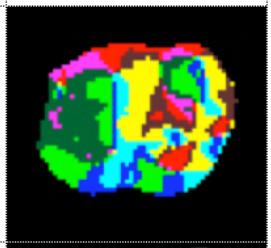
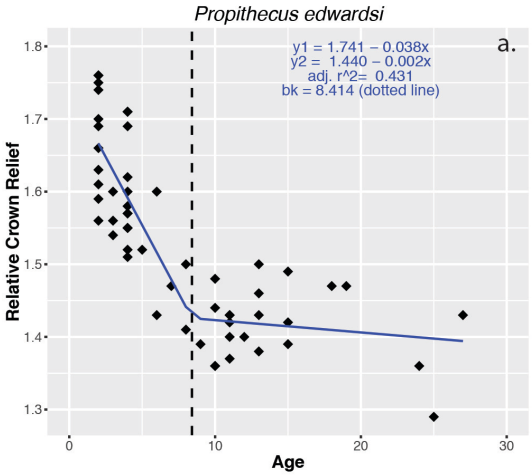
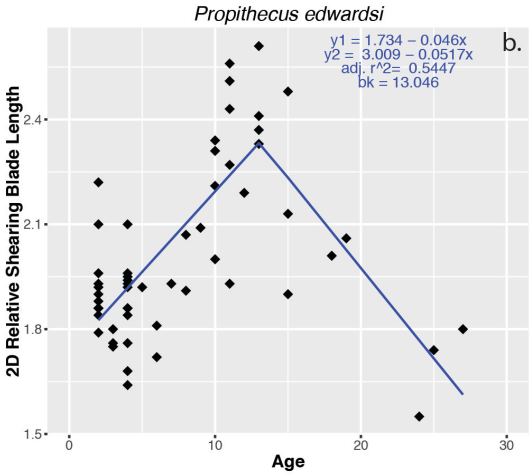
Variables	Definitions	Examples of DEM and Maps
Digital Elevation Model (DEM)	A raster-based digital reconstruction of the occlusal surface from which measurements and all other maps are generated. (Wheatly and Gillings, 2002)	
Slope	A measure of overall surface gradient. (Ungar & Williamson, 2000)	
Angularity (ANG)	A measure of the jaggedness of a surface and is the rate of change in slope across the occlusal surface. (Ungar & Williamson, 2000)	
Relief Index (RFI)	A measure of overall occlusal relief and is the ratio of the 3D and 2D surface area * 100 (Ungar & Williamson, 2000).	
Orientation Patch Counts Rotated (OPCR)	A measure of the overall complexity that sums the number of patches that slope in different directions; this is proportional to the number of "dental tools" available on an occlusal surface. (Evans et al., 2007; Evans & Jernvall, 2009)	
Percentage of Exposed Dentine (PED)	A measure of exposed dentine (i.e., gray regions) calculated as: (2D area of exposed dentine/total 2D occlusal surface area)*100.	

Figure 2.1. Summary of key dental topographic variables (Images are of a *G. gorilla* dp_4.)





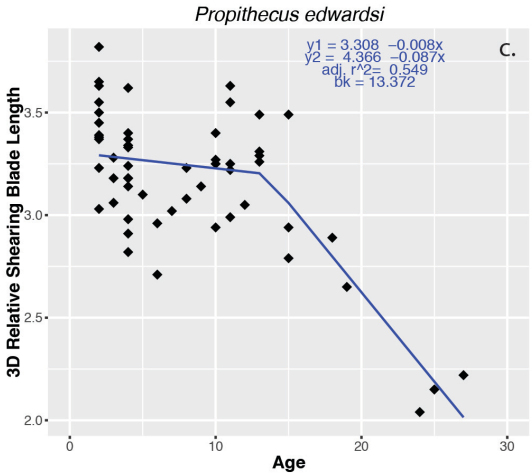


Figure 2.2 a-c. Scatterplots of best-fit models using King et al. (2005) data set. For Fig 2a, a dotted line was provided to clarify where the breakpoint occurred. Y1 provides the linear equation for the first line and y2 provides the linear equation for the second line.

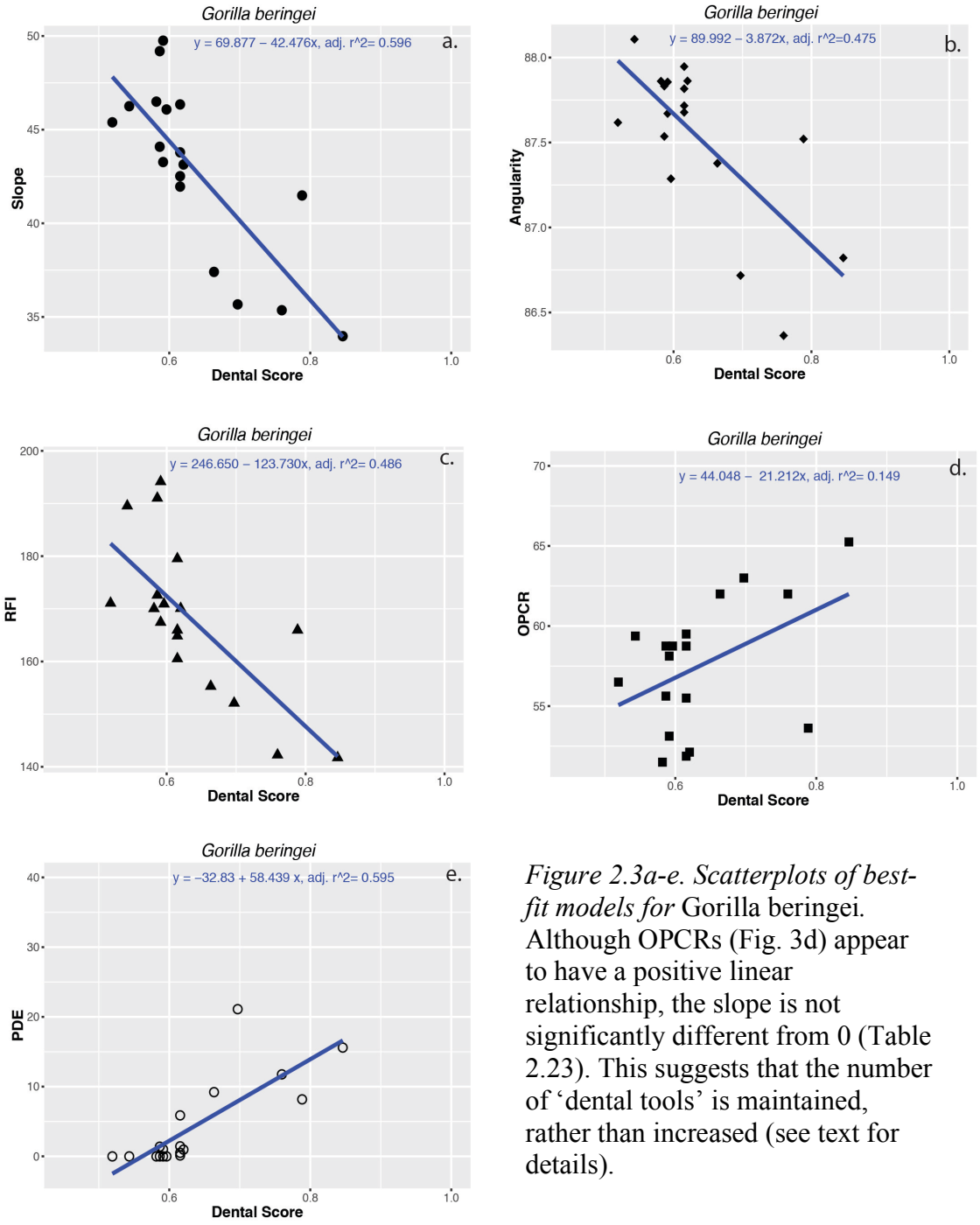


Figure 2.3a-e. Scatterplots of best-fit models for Gorilla beringei. Although OPCRs (Fig. 3d) appear to have a positive linear relationship, the slope is not significantly different from 0 (Table 2.23). This suggests that the number of 'dental tools' is maintained, rather than increased (see text for details).

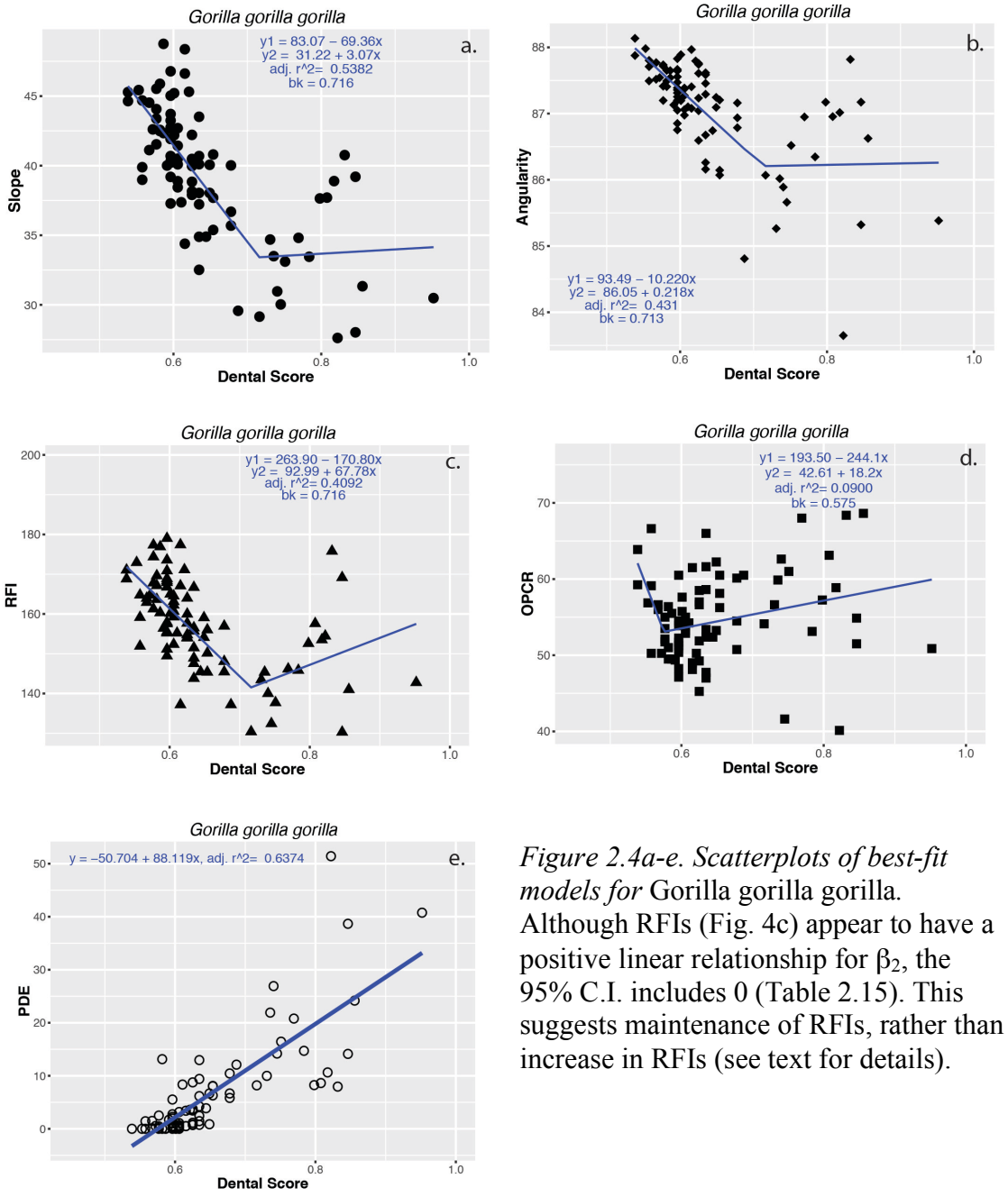


Figure 2.4a-e. Scatterplots of best-fit models for Gorilla gorilla gorilla. Although RFIs (Fig. 4c) appear to have a positive linear relationship for β_2, the 95% C.I. includes 0 (Table 2.15). This suggests maintenance of RFIs, rather than increase in RFIs (see text for details).

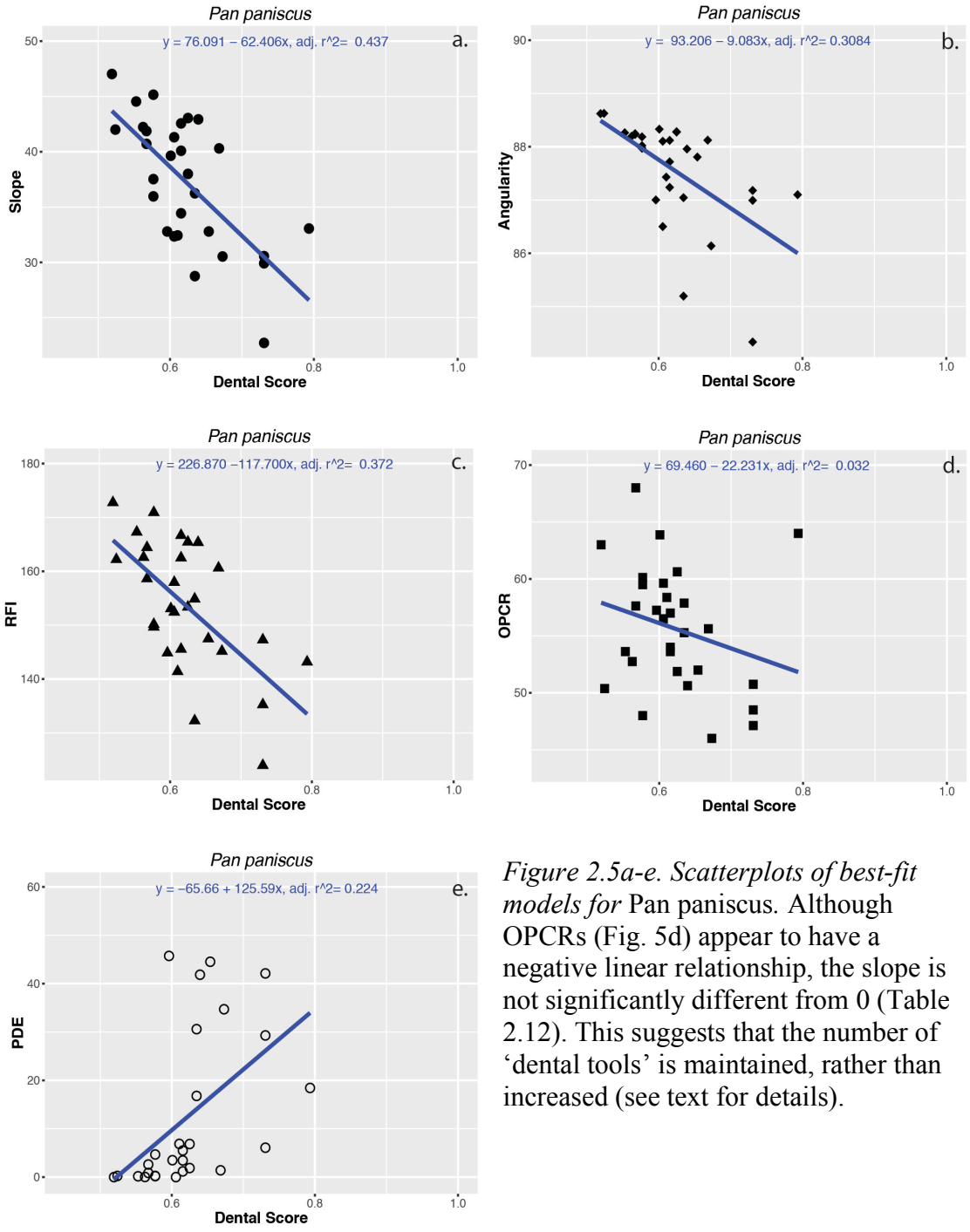


Figure 2.5a-e. Scatterplots of best-fit models for Pan paniscus. Although OPCRs (Fig. 5d) appear to have a negative linear relationship, the slope is not significantly different from 0 (Table 2.12). This suggests that the number of 'dental tools' is maintained, rather than increased (see text for details).

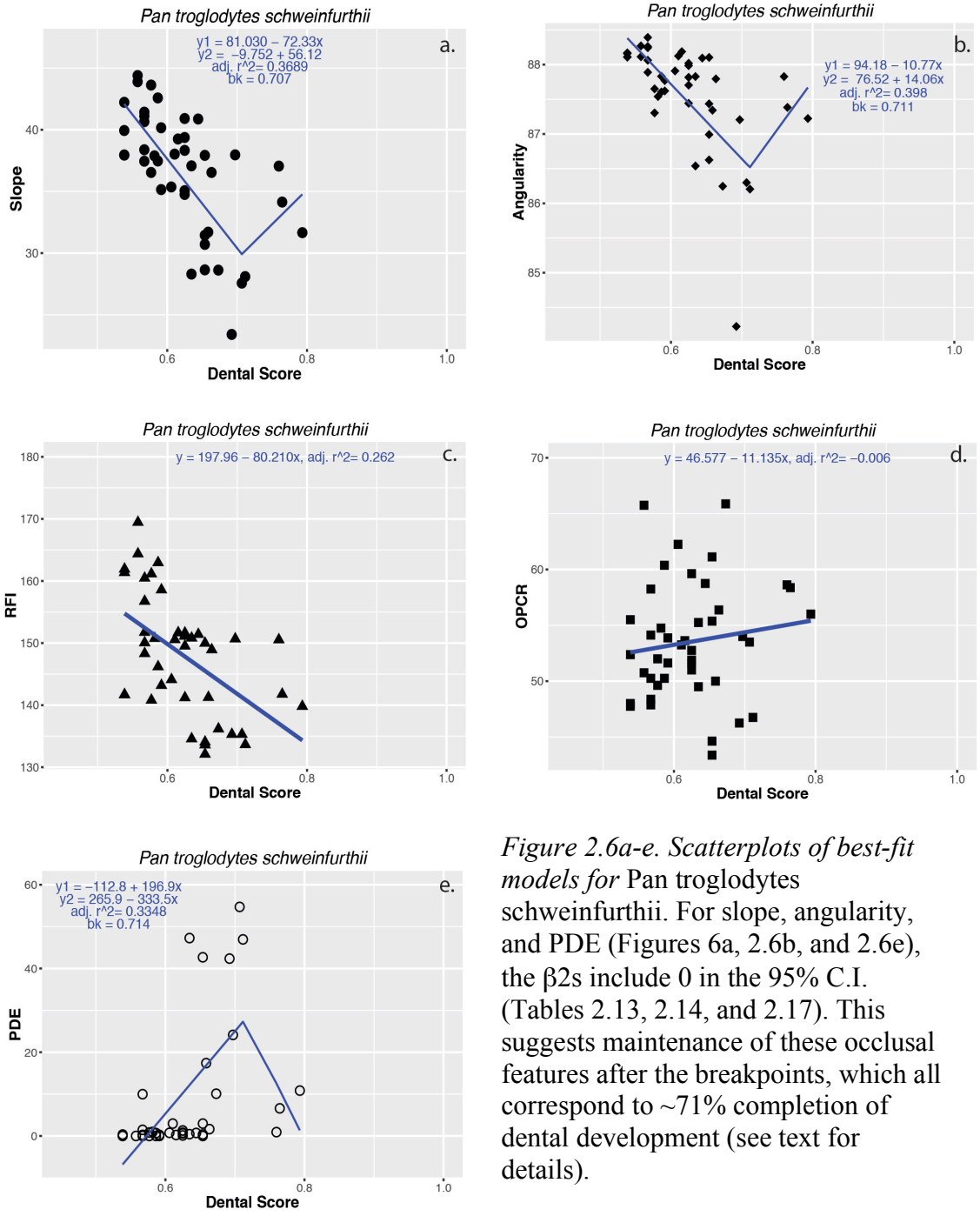


Figure 2.6a-e. Scatterplots of best-fit models for Pan troglodytes schweinfurthii. For slope, angularity, and PDE (Figures 6a, 2.6b, and 2.6e), the β2s include 0 in the 95% C.I. (Tables 2.13, 2.14, and 2.17). This suggests maintenance of these occlusal features after the breakpoints, which all correspond to ~71% completion of dental development (see text for details).

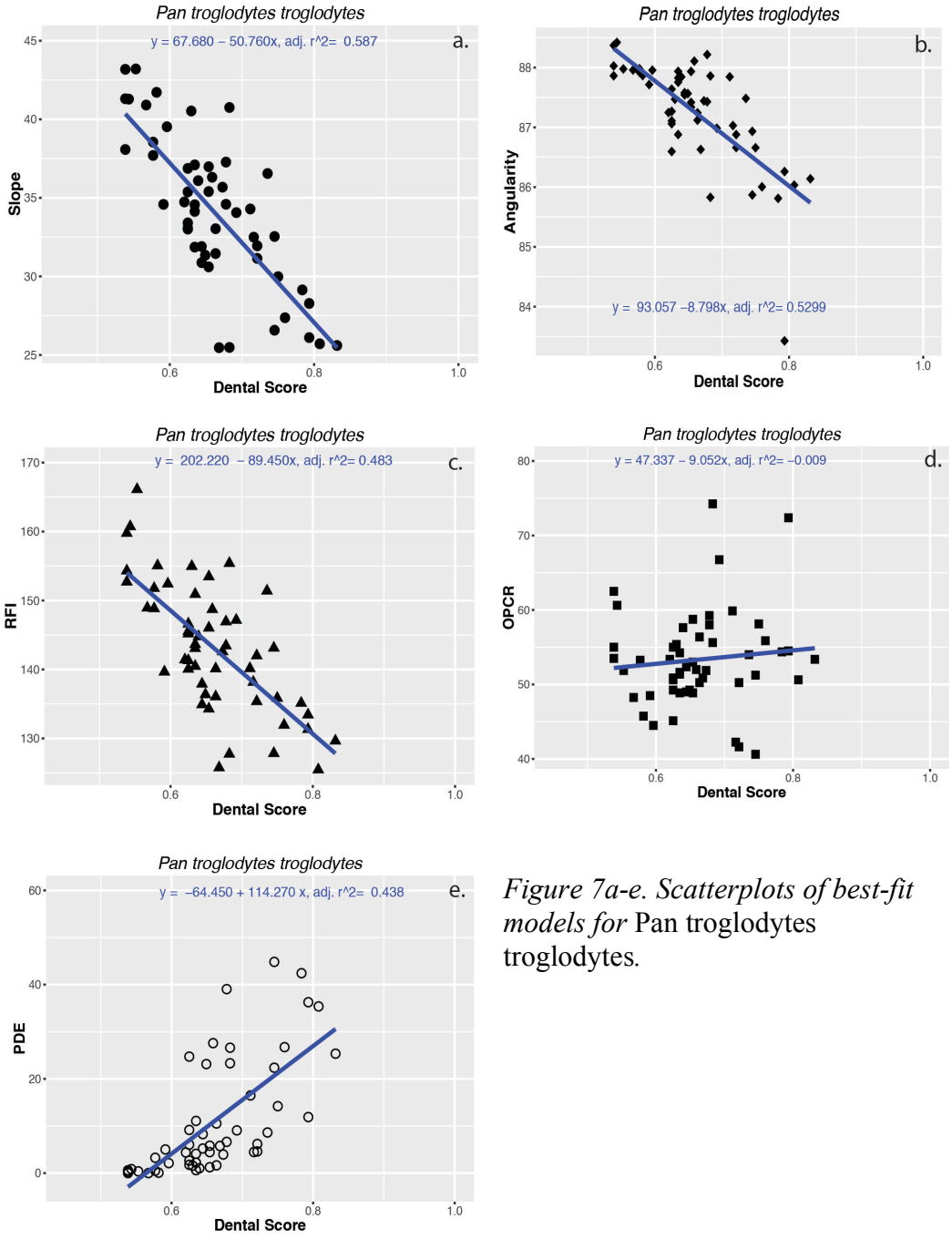


Figure 7a-e. Scatterplots of best-fit models for Pan troglodytes troglodytes.

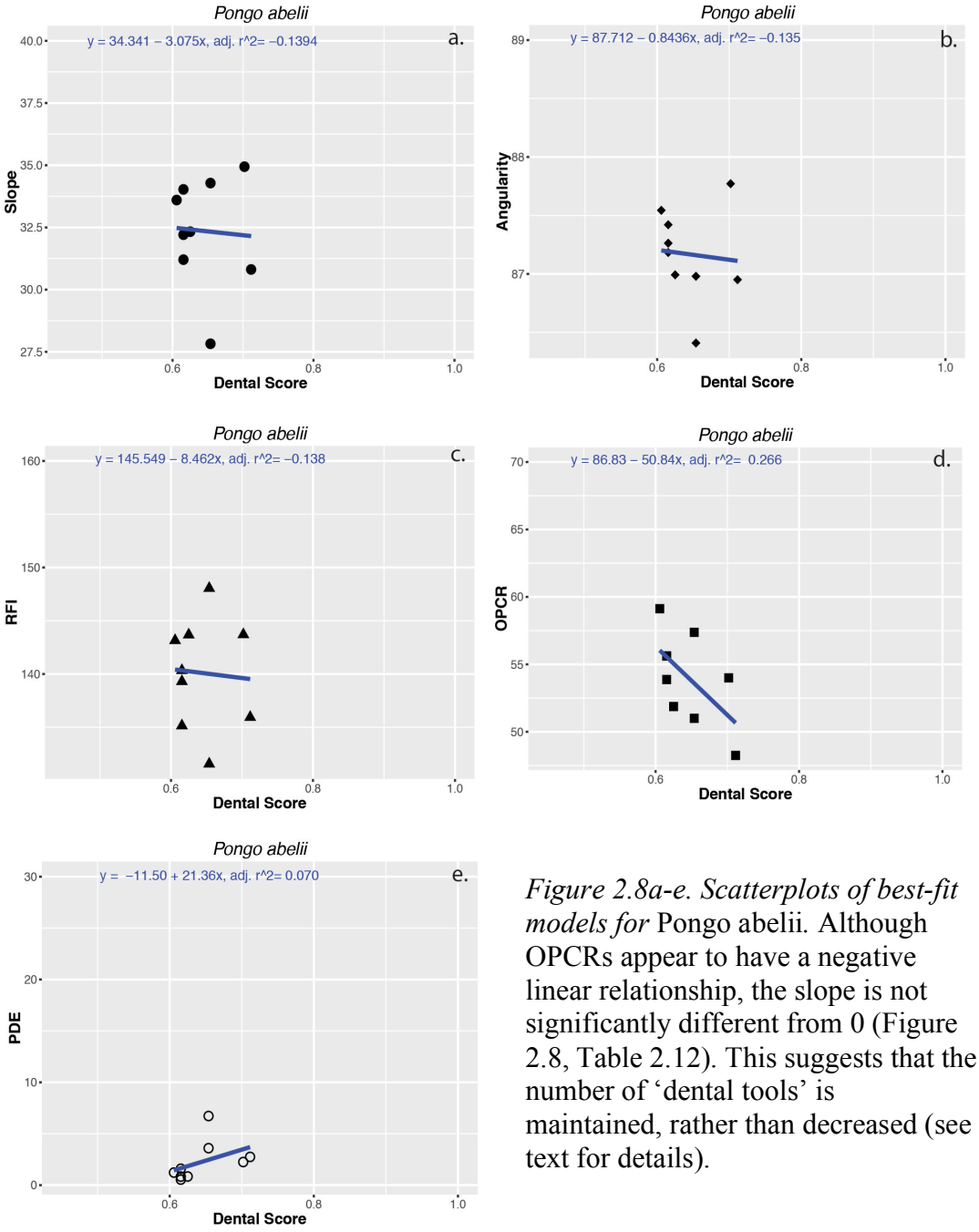


Figure 2.8a-e. Scatterplots of best-fit models for Pongo abelii. Although OPCRs appear to have a negative linear relationship, the slope is not significantly different from 0 (Figure 2.8, Table 2.12). This suggests that the number of 'dental tools' is maintained, rather than decreased (see text for details).

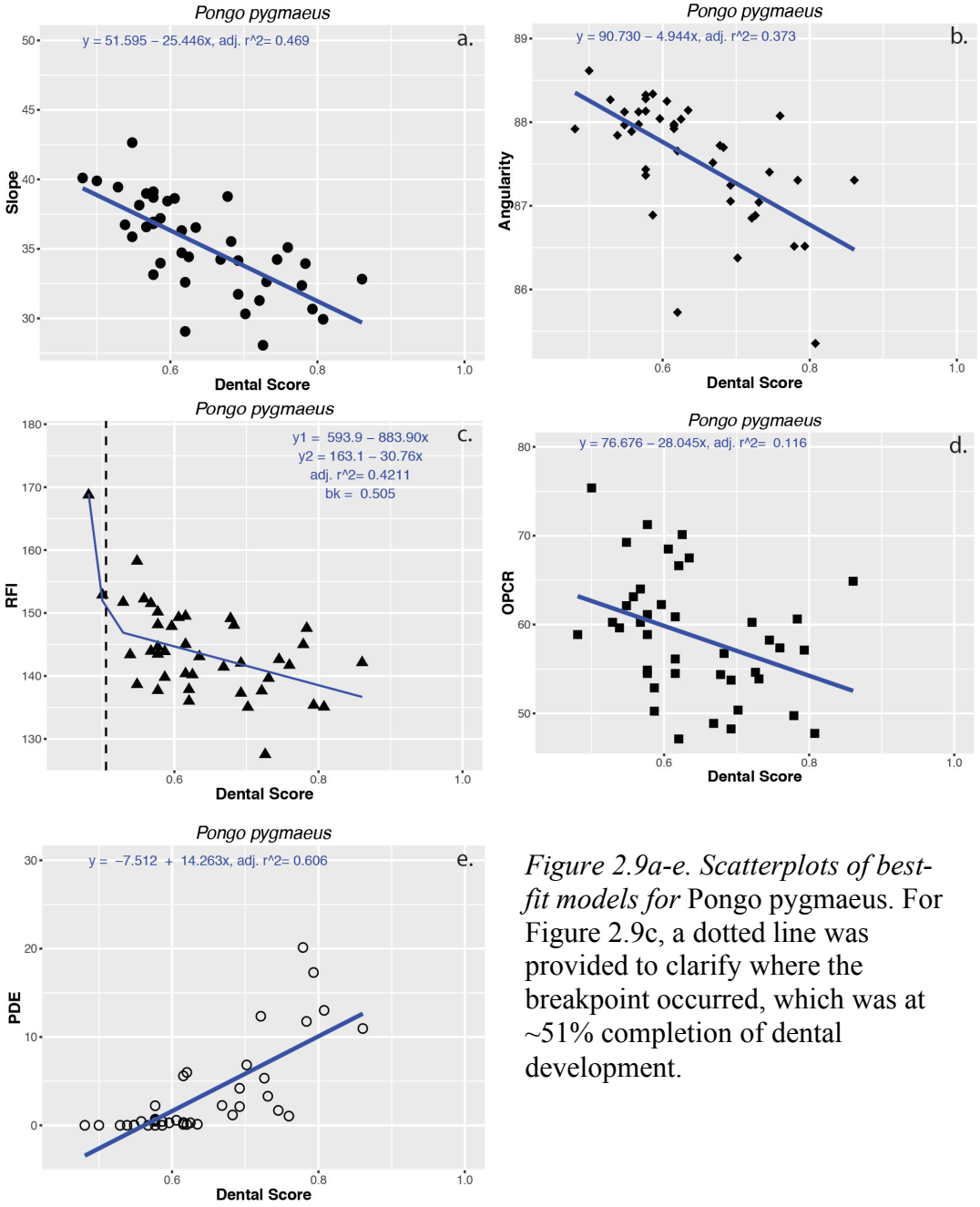


Figure 2.9a-e. Scatterplots of best-fit models for Pongo pygmaeus. For Figure 2.9c, a dotted line was provided to clarify where the breakpoint occurred, which was at ~51% completion of dental development.

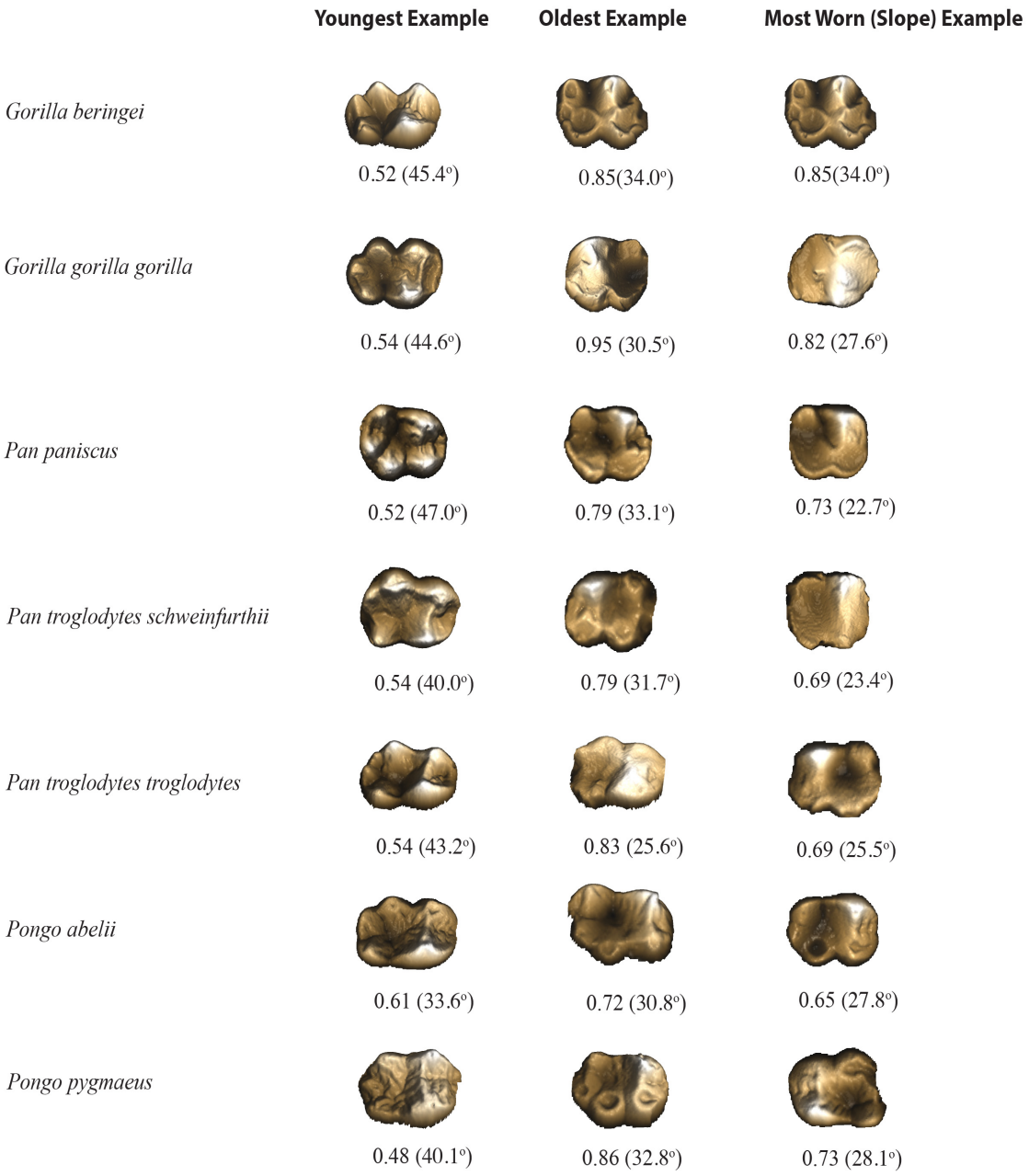


Figure 2.10. DEMS comparing the youngest and oldest individuals. Dental scores are listed below each DEM and the slope values are reported in parentheses. Individuals with the lowest slopes (i.e., most worn) are presented at the far right and the dental scores (i.e., relative age) are listed below the DEMs. In *Gorilla beringei*, the oldest and most worn example represents the same individual. This montage highlights the point that the most worn teeth do not necessarily represent the oldest individuals (see text for additional details).

CHAPTER 3

DOES WEAR ON THE MANDIBULAR FOURTH DECIDUOUS PREMOLAR (DP4) DEMARCATE AGE AT WEANING IN THE GREAT APES?

Abstract

Objectives: Along with dietary influences, Aiello et al. (1991) hypothesized that great ape species with higher percentages of dentine exposure (PDE) on the deciduous teeth weaned earlier than species with less PDE. Given the importance of weaning in the evolution of life histories, if this hypothesis is supported, then it might provide another avenue to estimate relative age at weaning in the hominin fossil record. The objective of this project is to test Aiello et al.'s (1991) hypothesis by analyzing dp_4 macrowear.

Material and Methods: Macrowear on the occlusal surfaces of dp4s from a cross-sectional sample of wild-shot juvenile specimens representing *Gorilla gorilla gorilla*, *Pan troglodytes schweinfurthii*, *Pan paniscus*, and *Pongo pygmaeus* were analyzed using dental topographic analytical techniques (N=199). Dp_4 occlusal wear (i.e., slope, angularity, relief index (RFI), orientation patch counts (OPCRs), and percentage of dentine exposure) was quantified.

Results: Rank-transformed MANOVA analyses demonstrate significant main effect differences among the four great ape species for various dental topographic measurements; however, the interactions between species and weaning status are only significant for ranked OPCRs. Follow-up discriminant function analyses for not weaned and weaned individuals suggest ranked OPCRs contribute only a small proportion of the overall variance.

Discussion: A direct test of Aiello et al.'s hypothesis was not possible because the weaning status was unknown for all individuals in this study. Indirect tests of

association suggest that dp_4 occlusal macrowear is not useful to estimate the relative timing of weaning in these four great ape species, suggesting that dp_4 macrowear has little to no utility to estimate the age at weaning for fossil hominins. Further research directions are discussed.

Introduction

Decades of comparative research on primates reveal that modern humans have an unusual life history profile. Modern humans exhibit a protracted growth, developmental, and reproductive schedule, but they wean offspring early relative to their body and brain size (e.g., Schultz, 1956; Martin et al., 1985; Bogin, 1999, Kaplan et al., 2000; Robson and Wood, 2008). Therefore, many palaeoanthropologists want to answer this question—*how* and *when* did the modern human life history profile, including early weaning, evolve (e.g., Smith, 1989; Smith, 1992a; Schwartz, 2012; Kelley and Schwartz, 2012; Kuzawa and Bragg, 2012; Austin et al., 2013; Smith, 2013; van Noordwijk et al., 2013)?

To ensure the survival of altricial young, humans have evolved a cooperative breeding strategy. Evolutionary anthropologists studying humans and callitrichids have documented how cooperative breeding promotes prosocial behaviors in childrearing practices, which, in turn, releases mothers from certain physiological constraints allowing them to reproduce more quickly (e.g., Burkart et al., 2009; Hrdy, 2009). Alloparenting contributions from group members, such as assistance from women past their reproductive years (e.g., grandmothers), enable younger women to divert their energy to produce more offspring (Hawkes et al., 1998; Hrdy, 2009). The cooperative breeding hypothesis explains *how* humans can raise energetically costly big-brained children for an extended time but wean them early (Isler and van Schaik,

2012). Still, it is unknown *when* early weaning and cooperative breeding evolved within the hominin lineage (e.g., Smith et al., 1995; Dean et al., 2001; Smith et al., 2007; Kelley and Schwartz, 2012; Schwartz, 2012; Smith, 2013).

Biogeochemical analyses are the most reliable method to track weaning (e.g., Humphrey et al., 2008a,b; Dirks et al., 2010; Clementz, 2012; Austin et al., 2013), but given the destructive nature of this approach its application to the fossil record is limited. Therefore, the estimation of age at weaning in extinct primate species primarily relies on statistical models describing the relationships between age at weaning, age at M_1 emergence, and brain size in extant primates (Smith, 1989; Smith et al., 1995; Kelley and Schwartz, 2012). Due to intra- and interspecific variation, the relationship between M_1 emergence and weaning is not uniform, and this is particularly true of the great apes (reviewed by Smith, 2013). While reported ages of M_1 emergence and age at weaning maintain a strong association at the species-level in some great apes (Kelley and Schwartz, 2010), studies at the population-level show that ape juveniles are not fully weaned until several years after the emergence of M_1 (Smith et al., 2013; Macho and Lee-Thorp, 2014). While incongruities between M_1 emergence and age at weaning may limit the utility of dental development to reconstruct the timing of weaning in hominins, perhaps the multiyear process of weaning is the most confounding variable when trying to develop a model that estimates weaning in extinct hominins.

For many primate species, including the great apes, weaning is a *process* rather than an *event*, making weaning difficult to define, document in the wild, and conduct intra- and interspecific comparisons (e.g., Lee, 1996; Godfrey et al., 2003; Humphrey, 2010; van, Noordwijk, et al., 2013). A general definition of *weaning* that highlights the idea that it is a *process*, rather than an *event*, brackets the time from

when infants start to supplement their diets with foods other than breast milk to when breast milk is no longer part of their dietary regime (i.e., fully weaned) (Lee, 1996; Langer, 2008). Unless specifically stated, the ages at weaning reported in the literature focus on the last observed instances of when juveniles suckled from their mothers. Paleontological reconstructions of age at weaning also focus on the time when a juvenile completely ceases to obtain nourishment in the form of mother's milk (e.g., Dean et al., 2001; Smith et al., 2007). Therefore, in this study, the term age at weaning is used to reference the time when juveniles completely cease to suckle (i.e., the weaning process is fully complete). For example, in *Pongo abelii* infants feed on breast milk until they start to supplement their diet with some solid foods at about 1-1.5 years of age (Table 3.1; citations therein). Infants and juveniles will increase their solid food intake but continue to suckle from their mothers until about 6 – 8 years of age. Therefore, the average age at weaning, which signifies a dietary shift of no longer incorporating breast milk, for *P. abelii* is ~ 7 years, but the range of variation for when *P. abelii* completes the weaning process is 6-8 years (Table 3.1). Figure 3.1 visually highlights both the inter- and intraspecific variation of when great ape juveniles cease to suckle (i.e., age at weaning), as the white-filled boxes extend for many years within a species and overlap with the other species of great apes. Despite the broad age ranges, there are still some discernible differences in the age at weaning among great apes. Although limited, the current data indicate that African apes regularly start to ingest supplemental foods at about 6-12 months of age, and, in comparison, infant orangutans delay the ingestion of supplemental foods for nearly 1.5 years (Table 3.1 and citations therein). In general, large-bodied mountain gorillas wean their offspring at about ~3.6 years of age, which on average, is earlier than *Pan spp.* or *Pongo spp.* (Figure 3.1 and Table 3.1). On average, *P. abelii* nurses longer

than any other ape (van Noordwijk and van Schaik, 2005), and the average age at weaning is ~7 years (Table 3.1 citations therein). However, as Figure 3.1 illustrates, some *Pan t. schweinfurthii* are not fully weaned until ~7.5 years of age, an age that falls well within the ranges for *P. abelii* (Figure 3.1). While the age ranges are useful, detailed data tracking weaning in individuals or sample standard deviations are rarely available in the literature. The lack of detailed data prevents studies, including this one, from utilizing uniform statistical markers of central tendency (e.g., means or medians) or other measures that quantify dispersion, such as coefficients of variation. Therefore, this study relies on the midpoint of the age ranges, denoted in Figure 3.1, to act as a proxy mean. When considering just the midpoint values (i.e., red bars in Figure 3.1), the ages at weaning in great apes follow a generalized relative pattern—mountain gorillas (*G .b. beringei*) wean the earliest, followed by the other gorillas (*G. g. gorilla*) and bonobos (*P. paniscus*), chimpanzees (*Pan spp.*), and, lastly, orangutans (*Pongo spp.*)

Figure 3.1 also includes the age at weaning in humans. Dettwyler (1995; 2004) considered various physiological markers (e.g., the age when children attain adult-like immune responses, dental development), primate life history data, and ethnographic data and concluded that the "natural age" for weaning in modern humans is 2.5-7 years. Observations of non-industrial human children suckling past the age of 4 is rare, and most children are weaned between 2-3 years (Sellen, 2001; Kennedy, 2005; Humphrey, 2010; Britton, 2015), which is the expected 'natural' age range based on primate scaling relationships with maternal body weight (Martin, 2007). While the range of 2-4 years for age at weaning in modern humans is much earlier than most of the great apes (Figure 3.1), the common age range for weaning in modern non-industrial humans is still broad and overlaps with both species of *Gorilla*

(Figure 3.1) rather than our closest living relatives, the chimpanzees.

In terms of dental development, Figure 3.1 visually highlights the dissociation of M_1 emergence and age at weaning for humans and chimpanzees. In humans, the emergence of M_1 occurs several years after weaning, but in *P. t. schweinfurthii*, M_1 emergence occurs *before* weaning (Smith et al., 2013). Although dental developmental data are limited, M_1 emergence coincides with ranges of age at weaning in *G. g. gorilla*, *P. paniscus*, and *P. pygmaeus* (Figure 3.1). Currently, no dental developmental data with absolute ages are available for *G. beringei* or *P. abelii*. I observed a museum note stating that a captive *P. abelii* individual died at ~6 years of age but the M_2 had not yet emerged; therefore, possibly, M_1 also emergences before weaning (i.e., the cessation of suckling) in *P. abelii*. Much of the research examining the relationships between weaning and dental development have focused on the M_1. Relatively few researchers have focused on the possible relationships between weaning and the deciduous dentition.

Aiello et al. (1991) observed that tooth wear on deciduous and mixed dentitions (i.e., both deciduous and some permanent teeth are present) might provide insight into the weaning patterns of great apes and, by extension, hominins. Aiello et al. (1991) noticed in *Pan*, *Pongo* and *Gorilla* specimens at similar stages of dental development, the deciduous teeth of gorillas had greater dentine exposure than either chimpanzees or orangutans. They hypothesized that the differences in occlusal wear found in gorillas might be due to an earlier age at weaning and a diet with a greater proportion of tough, fibrous foods. The application to the fossil record was intriguing, as Aiello et al. (1991) also observed that for juvenile hominins at similar dental developmental stages individuals attributed to *Paranthropus* had greater dentine exposure than those attributed to *Australopithecus*. Koufos and de Bonis (2004)

extended the application of deciduous tooth wear as a proxy for weaning to *Ouranopithecus macedoiniensis*, a large-bodied ape from the Miocene, and they suggested that the limited deciduous tooth wear observed on a juvenile might be due to delayed weaning.

Possible tooth wear differences related to life history have also been noted in Middle and Upper Palaeolithic hominins. Skinner (1997) documented that Upper Paleolithic modern humans had significantly more dentine exposure on the anterior deciduous teeth than Middle Paleolithic Neanderthals. He proposed that wear differences might be related to Upper Paleolithic humans ingesting supplementary foods earlier than Neanderthals, commencing the weaning process faster than the Neanderthals.

The above-mentioned studies focused on dentine exposure; however, there have been several technological advancements in the study of dental macrowear, which use 3D mapping software to quantify complex changes throughout occlusal wear (e.g., Zuccotti et al., 1998; Ungar and Williamson, 2000). These more advanced technologies, called dental topographic analyses, allow researchers to simultaneously explore wear differences among different species, assess broad dietary categories at various states of wear, and to assess if teeth wear in a manner that maintains functional efficiency (e.g., Ungar and M'Kirera, 2003; Dennis et al., 2004; King et al., 2005; Glowacka et al., In Press; Chapter 2). Until now, these advanced techniques have only been applied to molars and not the deciduous premolars. The purpose of this study is to explore whether deciduous tooth wear is a reliable marker for age at weaning in the great apes by utilizing these refined techniques to study occlusal wear patterns.

Hypotheses

The primary objective of this project is to test Aiello et al.'s (1991) hypothesis; however, a concrete test of whether the timing of weaning affects tooth wear requires samples from individuals where the weaning status is known (e.g., 'not weaned' vs. weaned). An extensive comparative data set that includes multiple great ape species where individuals with known weaning status are not easily acquired. Therefore, this study explores whether there is a potential association among relatively weaning categories, the state of dental development, and dp_4 wear.

To this aim, four species of great apes were analyzed: *G. g. gorilla*, *P. paniscus*, *P t. schweinfurthii*, and *P. pygmaeus* (bolded species in Figure 3.1). These species were selected because, compared to other great ape species, more data on their life history and dental development exists. Since museum records rarely include known ages, the stage of dental development is a useful proxy for age. Therefore, it was necessary to have both life history and dental developmental data for each species included in this study. Using the midpoints (as described above and see Figure 3.1) as a proxy for the mean age at weaning, I predict that because *G. g. gorilla* and *P. paniscus* wean earlier (with similar, younger midpoints), they will have more worn dp_4s than *P .t. schweinfurthii* and *P. pygmaeus* (two taxa that have similar, older midpoints).

The dp_4 is a good tooth-type to assess the Aiello et al., (1991) hypothesis. As reviewed in Chapter 2, we are now better able to quantify wear on molar occlusal surfaces. In comparison to the postcanine dentition, the anterior tooth-types (i.e., the incisors and canines) lack complex occlusal surfaces. Since this study focuses on the great apes, the dp_4 is preferred over the mandibular deciduous third premolar (dp_3)

because the dp_3 also plays an important role in the canine-honing complex (e.g., Swindler, 2002; Delezene and Kimbel, 2011).

The limited data available on African great apes suggests that the dp_4 emerges approximately three months *after* solid foods are first ingested (Table 3.1). Infant orangutans ingest solid foods as late as 1.5 years of age, which is much later than in African apes (Table 3.1). Considering that little to no data exist on the teething process in great apes, it is not clear how much these initial solid foods contribute to the infants' overall caloric intake. As Aiello et al. (1991) noted, across the great apes, the dp_4 is in functional occlusion for approximately the same amount of time, 6.2-6.4 years before it is replaced with a permanent P_4, on average, at ~7 years of age (Table 3.1 citations therein); however, dental developmental data tracking premolar development are extremely limited. With the exception of the earliest three months when apes start to mouth and intake solids foods, the dp_4 is present throughout the entire process of weaning in relation to the midpoint (i.e., the proxy mean for age at weaning) in all great apes species (Table 3.1 and Figure 3.1)

A concrete test of whether the timing of weaning affects tooth wear requires samples from individuals where the weaning status is known (e.g., 'not weaned' vs. weaned). Since these data are not readily available, this study relies on established methods that explore whether there is a potential association between relative weaning categories, the state of dental development, and dp4 wear. Similar methods have been used to explore whether tooth wear differentiates taxonomic and dietary categories (e.g., Ungar, 2007; Klukkert et al., 2012).

To test whether species that wean earlier exhibit more wear, it is important to address first whether unworn dp_4s are distinguishable among the great apes when using dental topographic analyses. There are two main reasons why it is useful to

assess whether dental topographic measurements for unworn occlusal surfaces are different among the species analyzed in this study. While perhaps obvious, the first reason is that teeth of various species look different. If the overarching goal of this project is to assess whether the amount of wear present on the dp_4 is related to the timing of weaning, it is necessary first to establish a baseline understanding of initial morphological dp_4 differences among the great apes. If the amount of wear present on the dp_4 is related to weaning, it is important to identify if that is truly a weaning signal or if wear differences are attributed to dietary differences or simply due to inherent morphological variation among species. In other words, how much of any interspecific variation tracked throughout wear should be attributed to morphological or dietary differences among the dp_4s rather to weaning? Ungar (2007) found that species-specific wear patterns were maintained throughout wear on the M_2s of gorillas, chimpanzees, and orangutans, but, when assessing wear, different molar positions may not be interchangeable (Bunn and Ungar, 2009).

To summarize, this paper addresses three questions to examine Aiello et al.'s (1991) hypothesis:

1) Are the occlusal surfaces of unworn dp_4s significantly different among the great apes species?
2) As defined by the proxy means (midpoints in Figure 3.1), do great apes species that wean at an earlier age have greater wear on their dp_4s at weaning?
3) Given limitations of the sample, associations between species and age at weaning were explored using the earliest reported ages at weaning, rather than the potentially arbitrary midpoints, by pooling some species. Therefore, the final question examined was do great apes species that have much earlier ages at weaning (i.e., *G. g. gorilla and P. paniscus*) have greater wear on their dp_4s

than species that wean much later (i.e., *P. t. schweinfurthii* and *P. pygmaeus*)?

Given previous research using dental topographic analyses, it is expected that the dp_4s with unworn occlusal surfaces should be distinguishable at the species-level. In addition, it is predicted that great apes with earlier ages at weaning (i.e., *G. g. gorilla* and *P. paniscus*) will have more wear than species that wean at later ages (i.e., *P. t. schweinfurthii* and *P. pygmaeus*).

Material and Method

Sample

Only great ape species with published data on age at weaning and dental development were analyzed in this study. For example, dental developmental data and age at weaning exists for *P. t. schweinfurthii*, but not for *P. t. troglodytes*; therefore, *P. t. troglodytes* was excluded from this study, but considered in the previous study (Chapter 2). Unfortunately, data are still limited for many of the great apes species, and so only four species were included: *G. g. gorilla*, *P. t. schweinfurthii, P. paniscus,* and *P. pygmaeus*.

The sample consists of a cross-sectional ontogenetic series for each great apes species compiled from nine museum collections: Anthropological Institute & Museum, Zurich, Switzerland; American Museum of Natural History, New York, USA; Cleveland Museum of Natural History, Cleveland, OH; Museum of Comparative Zoology, Cambridge, MA; Smithsonian Institution National Museum of Natural History, Washington, D.C.; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Royal Museum for Central African, Tervuren, Belgium;

Powell-Cotton Museum, Birchington, England; Zoological State Collection, Munich, Germany.

Except for two very young *P. pygmaeus* specimens, only wild-shot individuals were included to ensure that the occlusal wear analyzed was the result of a natural diet. The two captive *P. pygmaeus* specimens were retained in the sample, as they were good examples of unworn dp_4s. Museum records were carefully examined to ensure that species designations concurred with the current understanding of the geographic distributions of the great ape species (e.g., Won and Hey, 2005; Gonder et al., 2006; Macho and Lee-Thorp, 2014).

Molding techniques and casting procedures are outlined in Chapter 2. Using standard protocols, molds of dp_4s were collected using President Jet Plus, a standard material used to collect high-resolution molds of teeth. Casts were made using Fujirock, a gypsum-based material that reproduces high precision dental replicas. The occlusal surfaces of the casts were digitized at the highest possible resolution (50μm) using the Roland MDX-15 sensory probe. Point cloud data were imported into GRASS GIS v. 7.0 and Surfer v. 8.0 to generate raster-based digital elevation models (DEMs).

In GRASS GIS, DEMs were generated using the r.in.xyz module. To determine the occlusal plane on the DEM, the deepest point within the occlusal basin that maintained the full occlusal outline was located and any data points below that point were removed (e.g., Ungar, 2007; Glowacka et al., In Press). After cropping, all DEMS were smoothed using a 5x5 moving-window neighborhood analysis (r.neighbors module) to reduce artificial surfaces representations. The smoothing function was based on the cell value averages and constrained to the center cell of the moving window (Appendix B). From the smoothed DEMs, maps

for slope, angularity, and relief index (RFI) were generated and measured in GRASS GIS. These are the standard dental topographic variables used to quantify changes on the occlusal surface throughout wear (reviewed in Chapter 2). Slope measures the average steepness of the surface, and angularity (or delta slope) measure the rate of change in slope and assesses the overall jaggedness of the occlusal surface (Ungar and Williamson, 2000). Slope and angularity were collected in GRASS GIS using the r.slope.aspect module. RFI was calculated as [(3D surface area/2D surface)*100]. Surface area metrics (i.e., r.univariate module) for RFI were collected in GRASS GIS using 3D surface area (i.e., r.surf.area module) and the 2D surface area of the occlusal outline of the DEM, a commonly used approach in dental topographic studies (e.g., Boyer, 2008). Scripts written in Python automated the smoothing process and data collection of slope, angularity, and RFI measurements in GRASS GIS 7.0 (Appendix B). By automating this aspect of data collection, it helped to ensure that all steps were precisely replicated for each tooth included in this study.

The calculation of dentine exposure was also conducted in GRASS GIS. While visiting the museum collections, high-resolution digital photographs were taken of each dp_4 molded. A digital camera with a macro lens was mounted to a copy stand and leveled. The occlusal surface of the dp_4 was positioned, leveled, and aligned with a scale. Several photographs were taken of the surface in .jpg and raw formats, which maximized the possible resolution of the digital images. The high-resolution photographs were used as references to locate the areas of exposed dentine on the DEMS. Areas of exposed dentine were digitized on the occlusal surfaces of the smoothed DEMs in GRASS GIS v. 7.0. The tracings resulted in vector-based area maps. If multiple areas of exposed dentine were present, the 2D

traced area maps were summed. The total 2D surface area value was the same 2D surface area value used for the RFI. PDE was then calculated as a percentage (i.e., [(summed 2D area of exposed dentine/the total 2D surface of the occlusal surface)*100].

Point cloud data of the digitized occlusal surfaces were also imported into Surfer v. 8.0 and Surfer Manipulator to generate DEMs and collect orientated patch counts rotated (OPCR) measurements using standard methods (Evans et al., 2007; Evans and Jernvall, 2009). A minimum of three cells sloping in the same direction was required to designate a portion of the occlusal surface as a "patch." The number of patches is directly proportional to the number of dental tools available on the occlusal surface. Dental topographic occlusal measurements (i.e., slope, angularity, RFI, and OPRCs) are discussed in further detail in Chapter 2.

Assignment of Weaning Status

Despite decades of research, large-scale data sets for several life history variables, including age at weaning, are still lacking for most species of primates, including the great apes, which have been studied extensively compared to many other primate species. Larger data sets collected with more uniform methods would enable more precise statistical tests to examine inter- and intraspecific life history comparisons (Borries et al., 2013). Many of the deficiencies in life history data are simply due to the fact that primates, especially the great apes, have long lifespans with delayed ages at reproduction and extended weaning schedules (e.g., Hayssen, 1993; Martin, 2007; Wich et al., 2004). In addition, observational conditions are often very difficult. For example, it is nearly impossible to record the last moment a juvenile suckles from its mother. As previously discussed, weaning is a process in

apes. Since weaning is a process, there are other factors at play than just the amount of direct nutritional supplementation from the mother to infant. Suckling is an important bonding activity. Hence, in terms of suckling, when juveniles are older it is more difficult to distinguish between a young ape's need for nutritional supplementation or social bonding with the mother (reviewed in Chapter One). In addition, a mother's tolerance level for a protracted weaning process can also vary with her age and whether siblings are present or absent (e.g., Goodall, 1986). Given the several limitations mentioned, access to large interspecific comparative samples for age at weaning in wild, free-ranging ape populations simply do not exist yet; however, some data do exist. Table 3.1 summarizes age ranges at cessation of suckling (i.e., fully weaned), which were collected from the literature.

Historically, many field studies do not include data for individuals; they report the mean, median, or ranges. Therefore, it was not possible to calculate a mean, median, or coefficient of variation for age at weaning across the great apes species. In order to overcome this limitation, this study relied on the midpoint for the age ranges that are available (Figure 3.1 and Table 3.1). Using the earliest and oldest reported ages at weaning (i.e., cessation of suckling) from the literature, data were combined to generate a range of age at weaning for each great apes species. Many studies do not distinguish male and female differences, even though there may be some important differences that influence the age at weaning for different sexes (e.g., Goodall, 1986; Stoinski et al., 2013). In addition, since the sex of specimens are rarely available for infant and juvenile specimens housed in museum collections, and data on weaning differences among the sexes are not widespread, weaning data for males and females were pooled for this study.

The next challenge was to assign a weaning status to each individual included

in this study. For this study, each specimen was assigned as either 'not weaned' or 'weaned,' with weaned being the complete cessation of suckling. Since ages for museum specimens are unavailable for this sample, it was not possible to assign a weaning status by comparing known-aged specimens with reported weaning age ranges from the literature. Therefore, each individual was assigned a dental developmental score based on the emergence status of the M_1 and M_2s (Table 3.2). Only the $M_1$and M_2s were utilized because, although extremely limited, some absolute ages for M_1 emergence and M_2 emergence are available for some great ape species. Species data for ages at M_1 and M_2 emergence are presented in Figure 3.1 and Table 3.1.

As discussed, previous studies have found a strong statistical correlation between the age at M_1 emergence and age at weaning in several species of primates (Smith, 1989; 1992). In addition, there are strong correlations between the timing of M_1 dental development, including M_1 emergence, and the M_2 (e.g., Smith et al., 1994; Kavanagh et al., 2007). Recent observations by Smith et al. (2013) have found that the association between M_1 emergence and age at weaning is weak in *Pan t. schweinfurthii* and may have limited utility when estimating age at weaning. Despite the limitation of using M_1 emergence as a proxy for age at weaning for some primates, including humans and some lemurs (Chapter 4) the age at M_2 emergence may also provide some insight to estimate the age at weaning. Therefore, when possible, mean ages and ranges for M_1 and M_2 emergence were collected from the literature. Data collected via histological approaches were used as proxy means for M_1 or M_2 emergence (Figure 3.1). To code each individual specimen included in this study as either 'not weaned' or 'weaned,' the following approach was applied (see Table 3.1 and Figure 3.1 for reference):

1) Age ranges for the cessation of suckling were compiled from the literature and a midpoint was established (see above);
2) Absolute ages for M_1 and M_2 emergence for each species were compiled from the literature. When data were available, the age ranges for M_1 and M_2 emergence were reported. The age ranges are plotted in Figure 3.1.
3) Table 3.3 outlines the species-specific criteria used to assign each specimen a weaning status (i.e., 'not [fully] weaned' or "[fully] weaned"). Each specimen was assigned a weaning status based on the position of the M_1 and M_2 dental developmental score (Table 3.2) relative to the proxy average age for weaning, the complete cessation of suckling (i.e., the midpoint see Figure 3.1).

For example, a *G. g. gorilla* specimen (M117 from the Powell-Cotton Museum) exhibits an M_1 in the process of emerging above the alveolar margin but had not yet reached the occlusal plane; therefore, the M_1 was assigned a dental developmental score of 3. The M_2 had not emerged, but was visible in the crypt and was assigned a score of 2 (Table 3.2). Figure 3.1 shows that in *G. g. gorilla* M_1 emergence occurs before the midpoint [i.e., the average age at weaning]. Based on the midpoint and the M_1 emergence age ranges (Figure 3.1), any M_1 dental score (i.e., 1, 2, 3, or 4) for *G. g. gorilla* could occur prior to the midpoint. To account for the variation present in *G. g. gorilla* ages at weaning, the age ranges for the emergence of the M_2 were also referenced. Figure 3.1 illustrates how the emergence of M_2 slightly overlaps with the latest ages at the cessation of suckling; however, most of the age range for the emergence of M_2 occurs after the very latest ages reported in the literature for age at weaning. Based on the rules presented in Table 3.3, individuals with an M_2 score of 1 or 2 were scored 'not weaned.' Therefore, specimen M117 was assigned a status of

'not [fully] weaned' since the M_1 dental developmental score was a 3 and the M_2 dental developmental score was less than 3. For dental developmental scores and assigned weaning status for all specimens included in this study please refer to the raw data (Appendix A).

The goal of this paper is to identify whether dp_4 wear exhibits a weaning signal within a broad interspecific analysis among great apes— not to establish exact ages at M_1 and M_2 emergence relative to age at weaning. The approach used in this paper to assign a weaning status to each specimen can be improved upon with larger samples that include data on absolute ages at weaning, more data on dental developmental events (e.g., absolute ages at M_1 and M_2 emergence), and longitudinal records from wild populations (e.g., Smith et al., 2013). However, the benefit of this approach is that it attempts to account for the variation of age at weaning present among great apes species. In addition, by including M_2 dental developmental data, this approach also recognizes that the age at M_1 emergence is not always the best predictor of age at weaning within the great apes. Until exact chronological ages and weaning status are documented for several individuals, the use of relative dental development is currently the best nondestructive approach to explore the relationship between deciduous tooth wear and weaning in great apes. Table 3.4 presents the sample sizes for each species and assigned weaning category.

Analytical Methods

All statistical analyses were conducted in SPSS v. 23. To test whether unworn dp_4 occlusal surfaces are statistically different among great ape taxa, only individuals with an M_1 dental score of 1 or 2 (Table 3.2) were examined. One-way analysis of variance (ANOVA) tests were conducted. One-way ANOVAs use the variances to

test whether the means of a dependent variable are significantly different among taxonomic groups (Sokal and Rohlf, 1994; Field, 2009). One-way ANOVAs were conducted for each dependent variable (i.e., slope, angularity, RFI, OPCRs, and PDE) followed by *post hoc* comparison tests (i.e., Tukey HSD and Bonferroni correction). These tests only offered a preliminary assessment of the data. It is important to note that the dependent variables (i.e., slope, angularity, OPCRs, RFI, and PDE) often capture related information (Tables 2.24-2.30 in Chapter 2). For example, prominent molar crests are typical of highly folivorous or insectivorous animals and, as a result, these molars are likely to have higher slopes and RFI values than more frugivorous species (e.g., Boyer, 2008; Bunn et al., 2011). To investigate the combined effect these measures have on dp_4 wear and weaning, a multivariate technique was deemed more appropriate. Therefore, a multivariate analysis of variance (MANOVA) was conducted; however, the data set violated key assumptions (normality and heterogeneity of variances) that should be met for a MANOVA. To account for the violation of key assumptions, data were rank-transformed (Sokal and Rohlf, 1994; Field, 2009).

Rank-transformation of data is an established and frequently utilized technique to mitigate the problem of using parametric statistical methods with data that violate assumptions (Conover and Iman, 1981; Conover, 2012; Klukkert et al., 2012). Another benefit of ranking the occlusal wear measurements is that all of the measures are transformed to the same scale (Sokal and Rohlf, 1994; Field, 2009). To rank-transform the data, species were pooled and the occlusal measurements were ranked separately. For each measurement, each individual was ranked from the smallest to the largest. For example, the lowest slope value in the data set belongs to a bonobo and is 22.72 degrees. That individual, for slope, was assigned a rank value of

1. The second lowest slope value was 23.40 degrees and belongs to a chimpanzee. That individual, for slope, was assigned a rank value of 2. This process was automated in SPSS v. 23 and repeated for each dependent variable. The independent variables, species and weaning status, were not transformed. A two-way MANOVA was then conducted on the ranked data in SPSS v. 23. A two-way MANOVA analysis assesses the interaction of two independent variables, in this case species and weaning status, and how they relate with each other and the dependent variables. This particular statistical approach is useful to address the questions outlined in this study as it provides a method to distinguish differences that can be attributed to morphological differences across taxa and those that might be due to occlusal differences incurred during weaning. In other words, is there an interaction between weaning status and taxonomic status with various quantified values of occlusal wear? The MANOVA analysis was supplemented by two discriminant function analyses on the 'not weaned' group and then the 'weaned' group using the ranked data. A discriminant function analysis is a useful follow-up procedure as it assesses how well the explanatory variables classifies individuals for each group (Field, 2009).

A third discriminant function analysis was then used to assess how well the species separated based on the earliest reported age at weaning from the literature, rather than the midpoint. Given the broad, overlapping ranges for age at weaning in the great apes (Table 3.1 and Figure 3.1), the species were grouped into two broad categories: species that wean relatively early (i.e., *G. g. gorilla* and *P. paniscus*) and species that exhibit a relatively later age at weaning (i.e., *P. t. schweinfurthii* and *P. pygmaeus*).

Results

Question 1: *Are the occlusal surfaces of unworn dp_4s significantly different among the great apes species?*

The expectation was that the dental topographic values (i.e., slope, angularity, RFI, and OPCRs) for dp4s with unworn occlusal surfaces should be significantly different at least at the species-level. No differences were expected in the PDE, as the teeth analyzed were unworn. The predictions for the dental topographic values did not hold.

Table 3.5 presents the descriptive statistics for the unworn dp_4s. Levene's test for homogeneity of variances was insignificant for all the variables (Table 3.6), which indicates that the assumption for homogeneity of variances was met for the unworn dp_4 sample. One-way ANOVAs demonstrate significant differences among species for slope, angularity, RFIs, and OPCRs (Table 3.7). No significant differences were found for PDE (Table 3.7), which was expected since the dp_4s analyzed were unworn and, therefore, exhibited no dentine exposure. Although *post hoc* tests revealed significant differences among the species, the differences did not follow the expected pattern, as significant differences at the level of the species, or even the genus, were not consistently maintained (Table 3.8).

Question 2: *As defined by the proxy means (midpoints in Figure 3.1), do great apes species that wean at an earlier age have greater wear on their dp_4s at weaning?*

Based on Aiello et al.'s (1991) hypothesis, it was predicted that great apes with earlier ages at weaning (i.e., *G. g. gorilla* and *P. paniscus*) would have more wear (i.e., lower dental topographic values for slope, angularity, RFI, and OPCRs but higher values for PDE) than species that wean at later ages (i.e., *P. t. schweinfurthii* and *P. pygmaeus*). Overall, dp_4 macrowear, as measured in this study, was not a

reliable predictor of age at weaning; therefore, these predictions did not hold. Tables 3.9 and 3.10 present the descriptive statistics for the dependent variables for each weaning category. The untransformed data violated tests for equality of error variances (Table 3.11) as well as Box's M test for equality of covariance matrices (M=406.333, F(90,10626.126) = 3.970, $p< 0.001$). Therefore, as discussed, data were ranked before conducting MANOVAs.

Since sample sizes were unequal and assumptions were violated, Pillai's trace value was used (Field, 2009). Using Pillai's trace, there was a significant effect between taxonomic category and weaning status on the ranked measures of occlusal wear, V = 0.163, F(15, 561) = 2.15, $p = 0.007$ (Table 3.12). However, nearly all of the dependent variables had no significant interactions between taxonomic category and weaning status: slope (F(3,189) = 1.574, $p = 0.197$), angularity (F(3,189) = 1.046, $p = 0.373$), RFI (F(3,189) =1.260, $p = 0.289$, and PDE (F(3,189) = .0113, $p =0.953$). Only OPCRs yielded a significant interaction (F(3,189) = 3.757, $p=0.012$), which is discussed separately (see below). Separate univariate tests for differences among the taxonomic categories found that the same set of dependent variables (i.e., slope, angularity, RFI, and PDE) were significantly different, but OPCRs were not significantly different (Tables 3.13 and 3.14). Table 3.15 provides the *post hoc* comparison results. Comparisons between 'not weaned' and 'weaned' groups (species pooled) for slope, angularity, RFI, and PDE were significant, but not significant for OPCRs (Table 3.16).

Individual t-tests examined each species and dependent variables to assess the presence of any significant differences between 'not weaned' and 'weaned' groups (Table 3.17). While such an approach inflates Type 1 error, OPCRs consistently failed to reveal differences between the 'not weaned' and 'weaned' categories (Table

3.17). The significant differences found in most species and measurements do not necessarily indicate that these occlusal wear variables are truly picking-up a weaning signal. Rather, the significant differences between the 'not weaned' and weaned categories are likely a function of age, and simply due to that fact that the longer teeth are functioning in the oral cavity, the more likely the occlusal surfaces of the dp_4s are going to look different from occlusal surfaces that belong to younger individuals due to wear.

The results for ranked OPCRs are less straightforward. Of the wear variables examined in the MANOVA, only ranked OPCRs revealed a significant interaction ($F(3, 189) = 22433.26$, $p = 0.014$) between species and weaning status. However, tests for MANOVA between-subject effects found non-significant results for both taxonomic groups and weaning status. This suggests that for ranked OPCRs the weaning status is affecting the differences of states of ranked OPCR wear among the species.

Post hoc comparisons and interaction plots (Figure 3.2) for ranked OPCRs (Figure 3.2d) indicate that the significant interaction can mostly be attributed to gorillas in comparison with orangutans and bonobos. Ranked OPCRs decrease in bonobos and orangutans; however, the parallel nature of the lines indicates that weaning status does not play a role in producing the statistical difference between orangutans and bonobos. *G. g. gorilla* ranked OPCRs are higher in weaned individuals than 'not weaned' individuals. The line for gorillas is not parallel to the bonobos and orangutans; rather, it traverses both the bonobos and orangutans. Chimpanzees follow a pattern similar to gorillas, as ranked OPCRs are higher in weaned individuals than not weaned individuals. However, compared to the other species, chimpanzees have the lowest mean ranked OPCRs among both weaned and

'not weaned' groups. The interaction plot shows that the chimpanzee line does not traverse other lines suggesting that chimpanzees are not contributing to the observed interaction with ranked OPCRs and weaning.

A series of two-factor ranked MANOVAs on pairs of taxa were conducted as an additional follow-up to the ranked MANOVA that combined all taxa and dependent variables (Table 3.18). Although family pairwise errors can inflate the Type 1 error via such an approach, the goal was to assess if gorillas were primarily responsible for the significant interaction in the ranked OPCRs. These follow-up MANOVAs confirm that there are no significant interactions with chimpanzees and the other three species in this study. Bonobos and orangutans do not have a significant interaction. Therefore, the follow-up MANOVAs suggest that the significant interaction for taxa and weaning status in ranked OPCRs can be attributed to gorillas. The MANOVA was also supplemented with two discriminant function analyses that assessed how well the five dependent variables separated the species into the 'not weaned' group and the 'weaned' group (Figures 3.3 and 3.4). The first discriminant analysis focused on 'not weaned' individuals and revealed three discriminant functions. The first explained 87.2% of the variance, canonical R^2= 0.699, the second only explained 8.1% of the variance, canonical R^2=0.180, and the third function explained the remaining 4.8%, canonical R^2=0.115. In combination, these discriminant functions significantly differentiated the species (Table 3.19). The discriminant function coefficients and matrix structure are presented in Tables 3.20 and 3.21. Interestingly, out of the three discriminant functions, OPCRs loads almost entirely on the third function (Table 3.21), a function that only explains about 4.8% of the total variance within the 'not weaned' individuals. Classification results are presented in Table 3.22. In the group of 'not weaned' individuals, *P.t. schweinfurthii*

performed the most poorly with only 53.8% of the mandibular dp_4s being correctly classified. For *P. pygmaeus*, 76.9% were correctly classified, 80.0% of the bonobos, and 91.0 % of the gorillas.

The second discriminant function analysis assessed how well the five occlusal wear variables distinguished species in the weaned group, and this analysis also revealed three discriminant functions (Table 3.23). The first function explained 66.2% of the variance, canonical R^2= 0.494, the second function explained 28.2% of the variance, canonical R^2= 0.291, and the last function only explained 6.6% of the variance, canonical R^2= 0.082. In combination, only the first and second discriminant functions significantly differentiated the species (Table 3.23). The coefficients and matrix structure (Tables 3.24 and 3.25) show that ranked OPCRs do not dominate any particular function, unlike the 'not weaned' group. Rather, ranked angularity and ranked RFI dominated the loadings for functions 1 and 2. Classification results are presented in Table 3.26. For the weaned individuals, predicted group membership slightly decreased for gorillas, as 83.3% of the individuals were correctly identified. Bonobos dramatically decreased from 80.0% of 'not weaned' individuals being correctly classified to 52.6% of the weaned individuals being correctly classified. Interestingly, predicted group membership for *P. t. schweinfurthii* increased dramatically from 53.8% to 75.0% of the individuals being correctly classified. The other 25% were classified as orangutans. Lastly, 71.4% of the *P. pygmaeus* individuals were correctly classified.

Question 3: *Based on the earliest reported ages at weaning, do great apes species that have much earlier ages at weaning (i.e.,* G. g. gorilla *and* P. paniscus*) have greater wear on their dp_4s than species that wean at later ages (i.e.,* P. t. schweinfurthii *and* P. pygmaeus*)?*

A discriminant function analysis was conducted to assess how well the five occlusal variables distinguished groups based on the earlier reported ages at weaning, rather than the midpoint. This analysis only revealed one discriminant function, which explained ~100% of the variance, canonical $R^2 = .49$. This function significantly differentiated ($p \leq 0.05$) the group that had earlier weaning ages (i.e., gorillas and bonobos) from those with later weaning ages (i.e., chimpanzees and orangutans). The structure matrix reveled that ranked RFI loaded highly (r = 0.53) and ranked Angularity loaded also loaded highly, but in the opposite direction (r = -0.276). These results suggest that ranked RFI and ranked angularity might be the most relevant variables for sorting species into a 'weaning status' category. However, these are some of the key variables that distinguish the taxa themselves. Thus, whether a weaning signal is truly being identified or is due to morphological differences and/or dietary factors remains to be explored.

Discussion

The primary goal of this paper was to test if great ape species that wean at earlier ages exhibit greater wear on the occlusal surfaces of their dp_4s (Aiello et al., 1991). As discussed, a direct test was not possible since none of the individuals had a known weaning status at death. Therefore, the results of the study highlight possible associations between weaning status and dp_4 wear using states of relative dental developmental to serve as a an age proxy. In addition, since some aspects of dental development (e.g., M1 emergence) coincide with age at weaning in some great apes species (e.g., Smith, 1989; Schwartz and Kelley, 2010) then, at least for some species, dental development can serve as an estimate for age at weaning. However, the results of this study conclude that the state of occlusal macrowear on the dp_4s is unlikely to

be a reliable predictor for age at weaning in the great apes, and, by extension, macrowear on dp_4s is an unlikely to demarcate age at weaning in hominins.

The implicit assumption of this hypothesis is that the deciduous teeth from individuals that are weaned at an early age must bear the bulk of masticatory burdens for a longer time than individuals that have a late age at weaning. Since great apes have different absolute rates of dental development, comparisons of relative age categories (i.e., the same dental developmental stage) should offset the affect of absolute age differences. Albeit data are extremely limited, the dp_4s remain in functional occlusal for about the same length of time across great ape taxa, which also helps control for absolute age differences (e.g., Dean and Wood, 1981; Aiello et al., 1991; Smith et al., 1994). However, there are differences in M_1 and M_2 development, both in terms of absolute age and relative to age at weaning (Figure 3.1; Table 3.1 citations therein). Catlett (Chapter 2) found evidence of occlusal topographic maintenance for *P. t. schweinfurthii* and *G. g. gorilla* around the emergence of the M_2, suggesting that the presence of the M_2 may release the dp_4 from some of its masticatory burdens. Interestingly, the emergence of the M_2 may be a better predictor for age at weaning in *P. t. schweinfurthii*, as the age at weaning midpoint intersects with the age range of M_2 emergence in this species of chimpanzees (Figure 3.1). Perhaps, in this species alone, the dp4 macrowear patterns documented in Chapter 2 are the result of both being fully weaned and simultaneous emergence of M_2.

Ranked MANOVAs demonstrated that OPCRs seem to produce different wear signals than the other variables (e.g., slope, angularity, RFI, and PDE), but the gorillas primarily drove these differences. Catlett (Chapter 2) found that OPCRs *increased* in *G.g. gorilla*, which suggests that throughout wear the proportion of dental tools actually increased. Hence, the increase in the number of OPCRs is likely more related

to how the dp_4 wears, as the increase occurs prior to M1 emergence (Chapter 2; Tables 2.9 and 2.16), suggesting that, perhaps, the increase of 'dental tools' relates to an increase of supplementary foods rather than a byproduct of age at weaning.

Aiello et al. (1991) also noted that it was the gorillas with more wear differences when compared to orangutans and chimpanzees. Differences in diet seem like an obvious explanation. *G. g. gorilla* is noted for having a more folivorous diet when compared to chimpanzees; however, gorillas will incorporate large amounts of fruit and fallback on leaves when required (Yamagiwa and Basabose, 2009). Gorilla deciduous premolars and molars are noted for their taller crests and relatively thinner enamel (e.g., Swindler, 2002; Shellis et al., 1998), but even these features are no longer straightforward. For example, although gorilla teeth have morphological characteristics suggestive of a more folivorous diet compared to the other great apes, they still all share a similar broad hominoid morphology (e.g., Ankel-Simons, 2007). Both *Gorilla* and *Pan* are characterized by thin-enamel in the molars (e.g., Shellis et al., 2008). In an examination of the distribution of enamel thickness in molars, Skinner et al. (2015) report that *Gorilla* has thicker enamel in the occlusal basins than *Pan*. Broad comparative data on multiple primate taxa examining enamel thickness and the distribution of enamel in deciduous premolars does not yet exist, and so it is difficult to comfortably link gorilla dp_4 macrowear patterns to diet and enamel thickness. In addition, the precise causes of tooth wear are still debated (e.g., Lucas et al., 2014; reviewed in Chapter 1). Interestingly, the ape with one of the toughest diets, *G. beringei*, has some of lowest percentages of dentine exposure in both dp_4s and molars compared to other great apes (e.g., Elgart, 2010; Galbany et al., 2016; Chapter 2). Future research and the development of models that can test hypotheses about the relationship between deciduous tooth morphology, macrowear patterns, and the

mechanical properties of foods will help shed light on these important topics (e.g., Lucas, 2004; Berthaume, 2016).

Another key point to consider is the nature of the dental topographic variables themselves. In particular, slope, RFI, and OPCRs were developed to separate species into broad dietary categories, and these measures have been successfully applied to molars, particular the M_2 (e.g., Ungar and M'Kirera, 2003; M'Kirera and Ungar, 2003; Godfrey et al., 2012). In the great apes, researchers have divided the genera into broad dietary categories. For example, *Gorilla* has a highly folivorous diet, *Pan* has a more frugivorous diet, and *Pongo* has a highly frugivorous diet that incorporates hard foods (e.g., seeds, nuts). The great ape molars have successfully been segregated into these broad dietary categories and generic-designations (e.g., Ungar, 2007). Perhaps the most unexpected finding in the study was that the unworn dp_4s did not consistently segregate based on species or generic designations, and this is primarily due to the inclusion of the bonobos (Table 3.8). Slope was significantly different among the unworn dp_4s for gorillas, chimpanzees, and orangutans, a pattern that mirrors the one Ungar (2007) found for the M_2. Angularity and RFI were also significantly different among the gorillas, chimpanzees, and orangutans. Depending on the variable, the bonobos were rarely significantly different from any of the great ape taxa (Table 3.8). Perhaps, the bonobos possess a more generalized occlusal morphology when compared to the other great apes.

Interestingly, there were no significant differences in OPCRs between the unworn dp_4s of gorillas and orangutans, but, similar to the results of Ungar and M'Kirera (2003) for the M_2, there were significant differences between these two species in slope, angularity, and RFI. For OPCRs on unworn dp_4s, only *P. t. schweinfurthii* and *P. pygmaeus* were significant differently. *Gorilla* was not

significantly different from any of the other great apes species. The lack of OPCR differences suggests that great ape dp_4s start out with the same number of 'dental tools,' and it is the process of wear that alters the number of 'dental tools' on the dp_4s, as evidenced by the increase in OPCRs in *G. g. gorilla* (Chapter 2).

The third discriminant function analysis was conducted where individuals were not assigned a weaning status. Rather, species were pooled into two groups (i.e., earlier weaning vs. later weaning). The results suggested that RFI and angularity were the most useful variables to differentiate groups as having earlier weaning than later. However, again, tooth morphology, rather than the timing of weaning, may be driving these differences, as RFI and angularity were two dental topographic variables that successfully separated gorillas, chimpanzees, and orangutans in this sample.

Conclusion

The larger goal of this project was to test the hypothesis that species with earlier ages at weaning have more wear on the deciduous teeth than species that wean at later ages (Aiello et al., 1991). If the hypothesis were supported on an extant sample, then a study on the deciduous teeth of hominins testing for a weaning signal would be warranted (Wood and Schroer, 2012). The results of this study, which was based on associations among dental development and dental wear rather than known ages and weaning statuses, reject the hypothesis, at least as assessed by the macrowear patterns of the dp4s. Before the hypothesis is completely abandoned, there are a few points worth further consideration. Both Aiello et al. (1991) and Skinner (1997) noted wear differences on the anterior deciduous teeth. Since the anterior teeth are involved in different aspects of the digestive process, such as food acquisition, an assessment of anterior deciduous tooth wear relative to age at weaning is warranted.

Microwear is another avenue to evaluate the presence of a weaning signal. Microwear analyses measure how the microscopic texture changes on the occlusal surface. Extensive research has demonstrated that microscopic surface changes on the occlusal surface provide an excellent indicator of the foods the animal recently ingested (e.g., Walker et al., 1977; Teaford, 1988; Scott et al., 2012). Using microwear, Bullington (1991) analyzed mixed dentitions from an archaeological human population, and a similar study by Flanagan (2004; Godfrey et al., 2005a) was conducted in *Macaca fascicularis* and *Archaeolemur spp*. Both studies found that microwear trends dramatically differed upon the emergence of the first and second molars, suggesting microwear can potentially track ontogenetic changes in diet, such as age at weaning.

While analyses of the anterior dentition and microwear studies may be one way to assess the presence of a weaning signal, it is highly likely that only through an ontogenetic wear series can a weaning signal being reliably identified in the great apes. The reason for this statement is because the range of variation for age at weaning among the great apes is very broad. Great apes and humans are non-seasonal breeders that exhibit a highly flexible multiyear lactation strategy that reduces the mothers' energetic costs (van Noordwijk et al., 2013a,b; reviewed in Chapter 1). Non-seasonal breeders that lactate for several years, like apes, potentially have greater flexibility during periods of food scarcity since mothers can supplement the diet of an older juvenile not yet fully weaned (e.g., Macho and Lee-Thorp, 2014). In this context, the dietary role of breast milk in older juveniles could be classified as a fallback food (i.e., not a preferred food resources for the older juvenile) (Constantino and Wright, 2009). In socially complex animals, like the great apes, it is difficult to identify whether an older juvenile suckles to meet a nutritional need or to socially

bond with the mother (i.e., comfort-nursing) (Bateson, 1994; Kennedy, 2005; Dirks et al., 2010; Reitsema, 2012). In terms of reconstructing age at weaning in hominins, the most parsimonious conclusion is that hominins were similar to the great apes and humans—they were non-seasonal breeders with a multiyear lactation strategy (also characterized by a high degree of variation), and able to adapt to a variety of ecological habitats (e.g., Reed and Fish, 2005; Kuzawa et al., 2012). Future research on isotope ratios, and possibly microwear analyses, will help quantify the degree of variation for age at weaning that as been present throughout hominin evolution, and, eventually, lend insight into when cooperative breeding strategies evolved (e.g., Hrdy, 2009; Hill et al., 2009; van Noordwijk et al., 2013).

References

Aiello, LC., Montgomery, C. Dean, MC. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397-412.

Ankel-Simons, F. 2007. An Introduction to Primate Anatomy. San Diego: Academic Press.

Austin, C., Smith, TM., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D. , Hare, DJ., Doble, P., Eskenazi, B. Arora, M. 2013. Barium distributions in teeth reveal early-life dietary transitions in primates. Nature 498:216-219.

Bateson, P. 1994. The dynamics of parent-offspring relationships in mammals. Trends Ecol Evol 9:399-403.

Berthaume, MA. 2016. Food mechanical properties and dietary ecology. Am J Phys Anthropol 159:79-104.

Beynon, AD., Dean, MC. Reid, DJ. 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. Am J Phys Anthropol 86:189-203.

Bogin, B. 1999. Evolutionary perspective on human growth. Annu Rev Anthropol 28:109-153.

Borries, C., Gordon, AD. Koenig, A. 2013. Beware of primate life history data: a plea for data standards and a repository. PLOS One 8:1-12.

Boughner, JC., Dean, MC., Wilgenbusch, CS. 2012. Permanent tooth mineralization in bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*). Am J Phys Anthropol 149:560-571.

Boyer, DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Britton, K., Fuller, BT., Tüken, T., Mays, S., Richards, MP. 2015. Oxygen isotope analysis of human bone phosphate evidences weaning age in archaeological populations. Am J Phys Anthropol 157:226-241.

Breuer, T., Hockemba, MB., Olejniczak, C., Parnell, RJ. Stokes, EJ. 2009. Physical maturation, life-history classes and age estimates of free-ranging western gorillas-insights from Mbeli Bai, Republic of Congo. Am J Primatol 71:106-119.

Bullington, J. 1991. Deciduous dental microwear of prehistoric juveniles from the lower Illinois River Valley. Am J Phys Anthropol 84:59-73.

Bunn, JM., Ungar, PS. 2009. Dental topography and diets of four old world monkey species. Am J Primatol 71:466-477.

Bunn, JM., Boyer, DM., Lipman, Y., St Clair, EM., Jernvall, J. Daubechies, I. 2011. Comparing Dirichlet Normal Surface Energy of tooth crowns, a new technique of molar Shape quantification for dietary inference, with previous methods in isolation and in Combination. Am J Phys Anthropol 145:247-261.

Burkart, JM., Hrdy, SB. van Schaik, CP 2009. Cooperative breeding and human cognitive evolution. Evol Anthropol 18:175-186.

Clementz, M. T. 2012. New insight from old bones: Stable isotope analysis of fossil mammals. J Mammal 93:368-380.

Clark, CB. 1977. A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In: Skolnikoff, C., Poirier, FE., eds. Primate bio-social development: biological, social, and ecological determinants. New York: Garland. pp. 235–260.

Conover, WJ., Iman, RL. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124-129.

Conover, WJ. 2012. The rank transformation-an easy and intuitive way to connect many nonparametric methods to their parametric counterparts for seamless teaching introductory statistics courses. Computation Stat 4:432-438.

Constantino, PJ., Wright, BW. 2009. The importance of fallback foods in primate ecology and evolution. Am J Phys Anthropol 140:599-602.

Dean, C., Leakey, MG., Reid, D., Schrenk, F., Schwartz, GT., Stringer, C. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414:628-631.

Delezene, LK., Kimbel, WH. 2011. Evolution of the mandibular third premolar crown in early *Australopithecus.* J Hum Evol 60:711-730.

Dennis, JC., Ungar, PS., Teaford, MF. Glander, KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125:152-161.

Dettwyler, KA. 1995. A time to wean the hominind bluprint for the natural age of weaning in modern human populations. In: Stuart-Macadam, P, Dettwyler, KA., editors. Breastfeeding: biocultural perspectives. New York: Aldine de Gruyter. pp 39–73.

Dettwyler, KA. 2004. When to wean: biological versus cultural perspectives. Clin Obstet Gynecol 47:712-723.

Dirks, W., Humphrey, LT., Dean, MC. Jeffries, TE. 2010. The relationship of accentuated lines in enamel to weaning stress in juvenile baboons (*Papio hamadryas anubis*). Folia Primatol 81:207-223.

Elgart, AA. 2010. Dental wear, wear rate, and dental disease in the African apes. Am J Primatol 71:1-11.

Evans, AR., Wilson, GP., Fortelius, M. Jernvall, J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78-81.

Field, A. 2009. Discovering Statistics Using SPSS. Los Angeles: Sage.

Flanagan, EK. 2004. The ontogeny of dental use wear in *Archaeolemur* spp. and *Macaca fascicularis*. University of Massachusetts. Master's Thesis.

Fletcher, AW. 2001. Development of infant independence from the mother in the wild mountain gorillas. In: Robbins, MM., Sicotte, P. Stewart, KJ. et al., eds. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 153–183.

Fossey, D. 1979. Development of the mountain gorilla (*Gorilla gorilla beringei*): The first 36 months. Perspect Hum Evol 5:139-184.

Galbany, J., Imanizabayo, O., Romero, A., Vecellio, V., Glowacka, H., Cranfield, MR., Bromage, TG, Mudakikwa, A., Stoinski, TS, and McFarlin, S. 2016. Tooth wear and feeding ecology in mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol. Early View.

Glowacka, H, McFarlin, S., Catlett, KK., Mudakikawa, A., Bromage, TG., Cranfiled, MR., Stoinksi, TS., Schwartz, GT. In Press.. Molar wear in wild population of known-age mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol.

Godfrey, LR., Smaonds, KE., Jungers, WL., Sutherland, MR. 2003. Dental development and primate life histories. In: Kappeler, P. M., Pereira, M. E., editors. Primate life histories and socioecology. Chicago, London: University of Chicago Press, Chicago. p 177–203.

Godfrey, LR., Semprebon, GM., Schwartz, GT., Burney, DA., Jungers, WL., Flanagan, EK. 2005a. New insights into old lemurs: The trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825-854.

Gonder, MK., Disotell, T. Oates, J. 2006. New genetic evidence on the evolution of chimpanzee populations and implications for taxonomy. Int J Primatol 27:1103-1127.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Cambridge: Harvard University Press.

Harcourt, AH., Fossey, D., Stewart, KJ. Watts, DP. 1980. Reproduction in wild gorillas and some comparisons with chimpanzees. J Reprod Fertil Suppl 28:59-70.

Hawkes, K., O'Connell, JF., Jones, N.G.B., Alvarez, H. Charnov, EL. 1998. Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336-1339.

Hayssen, V. 1993. Empirical and theoretical constraints on the evolution of lactation. J Dairy Sci 76:3213-3233.

Hill, K., Barton, M. Hurtado, AM. 2009. The emergence of human uniqueness: Characters underlying behavioral modernity. Evol Anth 18:187-200.

Hrdy, SB. 2009. Mothers and others: The evolutionary origins of mutual understanding. Harvard University Press: Belknap Press.

Humphrey, L., Dirks, W., Dean, C. Jeffries.2008a. Tracking dietary transitions in weanling baboons (*Papio hamadryas anubis*) using strongtium/calcium ratios in enamel. Folia Primatol 79:197-212.

Humphrey, LT., Dean, CM., Jefferies, Teres E. Penn, M. 2008b. Unlocking evidence of early diet from tooth enamel. Proc Natl Acad Sci, USA 105:6834-6839.

Humphrey, LT. 2010. Weaning behaviour in human evolution. Semin Cell Dev Biol 21:453-461.

Isler, K., van Schaik, C. P. 2012. Allomaternal care, life history and brain size evolution in mammals J Hum Evol 63:52-63.

Jaeggi, AV., van, N., Maria A. van Schaik, CP. 2008. Begging for information: Mother-offspring food sharing among wild Bornean orangutans. Am J Primatol 70:533-541.

Jaeggi, AV., Dunkel, LP., Noordwijk, MAV., Wich, SA., Sura, AAL, van Schaik, CP. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. Am J Primatol 72:62-71.

Kano, T. 1989. The sexual behavior of pygmy chimpanzees. In: Heltne, PG., Marquardt, L., eds. Understanding chimpanzees. Cambridge: Harvard University Press. p 176–183.

Kaplan, H., Hill, K., Lancaster, J. Hurtado, AM. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. Evol Anthropol 9:156-185.

Kavanagh, KD., Evans, A. R. Jernvall, J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449:427-432.

Kelley, J., Schwartz, GT. 2012. Life-history inference in the early hominins *Australopithecus* and *Paranthropus.* Int J Primatol 1-32.

Kelley, J., Schwartz, GT. 2010. Dental development and life history in living African and Asian apes. Proc Natl Acad Sci USA 107:1035-1040.

Kennedy, GE. 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. J Hum Evol 48:123-145.

King, SJ. 2004. Relative timing of ontogenetic events in primates. J of Zool 264:267-280.

King, SJ., Arrigo-Nelson, SJ., Pochron, ST., Semprebon, GM., Godfrey, LR., Wright, PC. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci, USA 102:16579-16583.

Klukkert, ZS., Teaford, MF. Ungar, PS. 2012. A dental topographic analysis of chimpanzees. Am J Phys Anthropol 148:276-284.

Kuroda, S. 1989. Developmental retardation and behavioral characteristics of pygmy chimpanzees. In: Heltne, PG., Marquardt, L., editors. Understanding chimpanzees. Cambridge: Harvard University Press. pp 184–193.

Kuzawa, CW., Bragg, JM. 2012. Plasticity in human life history strategy implications for contemporary human variation and the evolution of genus *Homo.* Curr Anthropol 53:S369 S382.

Langer, P. 2008. The phases of maternal investment of eutherian mammals. Zoology 111:148-162.

Lee, PC. 1996. The meanings of weaning: growth, lactation, and life history. Evol Anth 5:87-98.

Lucas, PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press.

Lucas, PW., Casteren, AV., Al-Fadhalah, K., Almusallam, AS., Henry, AG., Michael, S. 2014. The role of dust, grit and phytoliths in tooth wear. Annales Zoologici Fennici Annales Zoologici Fennici 51:143-152.

Macho, GA., Lee-Thorp, JA. 2014. Niche partitioning in sympatric *Gorilla* and *Pan* from Cameroon: implications for life history strategies and for reconstructing the evolution of hominin life history. Plos One 9:e102794.

Martin, RD., Maclarnon, AM. 1985. Gestation period, neonatal size and maternal investment in placental mammals. Nature 313:220-223.

Martin, R.D. 2007. The evolution of human reproduction: A primatological perspective. Yrbk Phys Anthropol 134:59-84.

M'Kirera, F.,Ungar, PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla.* Am J Primatol 60:31-41.

Nowell, AA., Fletcher, AW. 2007. Development of independence from the mother in *Gorilla gorilla gorilla.* Int J Primatol 28:441-455.

Pusey, AEE. 1983. Mother offspring relationships in chimpanzees after weaning. Anim Behav 31:363-377.

Ramirez-Rozzi, F., Lacruz, R. 2007. Histological study of an upper incisor and molar of a bonobo (*Pan paniscus*) individual. In: Bailey, SE., Hublin, JJ., editors. Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Dordrecht, the Netherlands: Springer. Pp. 163–176.

Reed, KE and Fish, JL. 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, DK and van Schaik ,CP. Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates. Cambridge: Cambridge University Press, p. 489-518.

Reitsema, LJ. 2012. Introducing fecal stable isotope analysis in primate weaning studies. Am J Primatol 74:926-939.

Robson, SL., Wood, B. 2008. Hominin life history: Reconstruction and evolution. J Anat 212:394-425.

Schultz, AH. 1956. Postembryonic age changes. Primatologia 1:887-964.

Schwartz, GT. 2012. Growth, development, and life history throughout the evolution of *Homo*. Curr Anthropol 53:S395-S408.

Scott, RS., Teaford, MF. Ungar, PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Sellen, DW. 2001. Comparison of infant feeding patterns reported for nonindustralised populations with current recommendations. J Nutr 131:2707-2715.

Shellis, RP., Beynon, AD., Reid, DJ. Hiiemae, KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507-522.

Skinner, M. 1997. Dental wear in immature late Pleistocene European hominines. J Arch Sci 24:677-700.

Smith, BH. 1989. Dental development as a measure of life history in primates. Evolution 43:683-688.

Smith, BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:134-142.

Smith, BH., Crummett, TL. Brandt, KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yrbk Phys Anthropol 37:177-231.

Smith, BH., Boesch, C. 2011. Mortality and the magnitude of the "wild effect" in chimpanzee tooth emergence. J Hum Evol 60:34-46.

Smith, RJ., Gannon, PJ. Smith, BH. 1995. Ontogeny of australopithecines and early *Homo* - evidence from cranial capacity and dental eruption. J Hum Evol 29:155-168.

Smith, TM., Tafforeau, P., Reid, D. J., Grun, R., Eggins, S., Boutakiout, M. 2007. From the cover: Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci USA 104:6128-6133.

Smith, TM. 2013. Teeth and human life-history evolution. Annu Rev Anthropol 42:191-208.

Smith, TM., Machanda, Z., Bernard, AB., Donovan, RM., Papakyrikos, AM., Muller, MN, Wrangham, R. W.2013. First molar eruption, weaning, and life history in living wild chimpanzees. Proc Natl Acad Sci 110:2787-2791

Sokal, RR., Rohlf, JF. 1994. Biometry: The principles and practices of statistics in biological research. (3rd ed.). New York: W.H. Freeman and Co.

Stewart, KJ. 1988. Suckling and lactational anestrus in wild gorilla (*Gorilla gorilla*). JReprod Fertil 83:627-634.

Stoinski, TS., Perdue, B., Breuer, T. Hoff, MP. 2013. Variability in the developmental life history of the genus *Gorilla.* Am J Phys Anthropol 1-8.

Swindler, DR. 2002. Primate dentition: an introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

Teaford, M. F. 1988. A review of dental microwear and diet in modern mammals. Scanning Microsc 2:1149-1166.

Tutin, CEG., McGinnis, PR. 1981. Chimpanzee reproduction in the wild. In: Graham, C. E., ed. Reproductive biology for the great apes: Comparative and biomedical perspectives. New York: Academic Press. p 239–264.

Ungar, P., Williamson, M. 2000. Exploring the effects of tooth wear on functional morphology: A preliminary study using dental topographic analysis. http://palaeo-electronica.org/2000_1/gorilla/issue1_00.htm.

Ungar, PS. 2007. Dental topography and human evolution. In: Bailey, SE., Hublin, JJ., editors. Dental perspectives on human evolution: state of the art research in dental paleoanthropology. Dordrechet: Springer. p 321–344.

Ungar, PS., M'Kirera, F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. P Natl Acad Sci USA 100:3874-3877.

van Noordwijk, MA., van Schaik, CP. 2005. Development of ecological competence in Sumatran orangutans. Am J Phys Anthropol 127:79-94.

van Noordwijk, MA., Sauren, SEB., Nuzuar, AA., Morrogh-Bernard, HC., Utami Atmoko, SS. van Schaik, CP. 2009. Development of independence. In: Wich, SA., Utami, SS., Mitra Setia, T., van Schaik, C. editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 189–204.

van Noordwijk, MA, Willems, EP., Atmoko, SSU., Kuzawa, CW. van Schaik, CP. 2013. Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). Behav Ecol Sociobiol 67:805-814.

van Noordwijk., Kuzawa , MA., van Schaik, CP. 2013. The evolution of the patterning of human lactation: a comparative perspective. Evol Anthropol 22:202-212.

Walker, A., Hoeck, HN. Perez, L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201:908-910.

Watts, DP. 1991. Mountain gorilla reproduction and sexual behavior. Am J Primatol 24:211-225.

Wich, SA., Utami-Atmoko, SS., Setia, TM., Rijksen, HD., Schurmann, C., van Hooff, JA. 2004. Life history of wild sumatran orangutans (*Pongo abelii*). J Hum Evol 47:385-398.

Won, YJ., Hey, J. 2005. Divergence population genetics of chimpanzees. Mol Biol Evol 22:297-307.

Wood, B., Schroer, K. 2012. Reconstructing the diet of an extinct hominin taxon: The role of extant primate models. Int J Primatol 33:716-742.

Yamagiwa, J., Basabose, A. K. 2009. Fallback foods and dietary partitioning among *Pan* and *Gorilla.* Am J Phys Anthropol 140:739-750.

Zihlman, A., Bolter, D. Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. Proc Natl Acad Sci USA 101:10541-10543.

Zuccotti, LF., Williamson, MD., Limp, WF. Ungar, PS. 1998. Technical note: Modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107:137-142.

Table 3.1. Summary of relevant life history and dental developmental data

	Gorilla beringei beringei	*Gorilla gorilla gorilla*	*Pan troglodytes schweinfurthii*	*Pan paniscus*	*Pongo pygmaeus*	*Pongo abelii*
First Intake of Solid Food[1]	1-2 months mouthing; 6-12 months gnaw on foods but do not prepare foods		~ 6 -12 mos.		~ 1 -1.5 years	~1-1.5 years
Age at Weaning[2] (yrs.)	~3.6 (1.8-5.2)	~ 4.6 (3.0-6.1)	~5.32 (4.17 - 6.67)	~ 4.0	~5.5 (5.0-6.0)	~7.0 (6.0-8.0)
Age at dp_4 emergence (yrs.) [3]	~0.756		~0.750		0.808	
Age at P_4 emergence (yrs.)[4]	~7.14 (5.9-8.4)		~7.58 (6.08-9.08)		~7.0 (6.0-8.0)	
Age at M_1 emergence (yrs.)[5]	Unknown	3.0-4.0	2.52-3.75	4.77*	4.6	Unknown
Length of dp_4 use (yrs.)[6]	~6.38		~6.83		~6.19	
Age M_2 emergence[5]	Unknown	5.7-7.5	5.58-7.33**	~6.5***	Unknown	> 6 years****

Some data are pooled at the level of the genus, indicted by the merged cells, due to lack of data. [1]Clark, 1977; Fossey, 1979; van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2009 [2] Harcourt et al., 1980; Tutin and McGinnis, 1981; Pusey, 1983; Stewart, 1988; Kuroda, 1989; Watts, 1991; Kano, 1989; Fletcher, 2001; Wich et al., 2004; van Noordwijk and van Schaik, 2005; Nowell and Fletcher, 2007; Jaeggi et al., 2008; Breuer et al., 2009 Jaeggi et al., 2010; Stoinski et al., 2013; van Noordwijk et al., 2013 [4]Smith et al., 1994[5] [4]Smith et al., 1994; Zihlman et al., 2004; Ramirez-Rozzi and LaCruz, 2007; Kelley and Schwartz, 2010; Smith and Boesch, 2011 [6]Difference between age at P_4 emergence and age at dp_4 emergence: Smith et al., 1994.* The value reported is for the maxillary M1. **Value estimated from *P. troglodytes* sexes pooled. ***Values estimated from *P. troglodytes* as Boughner et al., 2012 report no difference in tooth mineralization between *P. troglodytes* and *P. paniscus*. ****For one captive individual aged 6 years and 12 days old at death, the M_2 had not emerged.

Table 3.2. Dental developmental scoring system (based on King, 2004)

Score	Developmental state of M_1 and M_2 tooth
1	Tooth not visible
2	Visible in crypt
3	Piercing or emerging above alveolar bone
4	Fully emerged and level to occlusal plane

Table 3.3. Binary coding rules for weaning status (see Figure 3.1 and text for details for age at weaning definition).

Taxa	Does the range of M_1 emergence ages overlap with the average age at weaning (i.e., the midpoint)?	Does the range of M_2 emergence ages overlap with average age at weaning (i.e., the midpoint)?	Weaning Status Coding Rules*
Gorilla gorilla gorilla	No. M_1 emerges before the midpoint. Therefore, any M_1 value of 1,2, 3, or 4 may occur prior to the midpoint. This is consistent with Macho and Lee-Thorp, 2014.	No. M_2 emerges after the midpoint. Therefore, any M_2 dental score value (i.e., 1,2, 3, or 4) could occur after the midpoint. However, M_2 emergence ranges overlaps with the later ranges of age at weaning.	If $M_1 \leq 4$ and M_1 is ≥ 3, code for weaned. Otherwise, code for not weaned.
Pan troglodytes schweinfurthii	No. M_1 emerges before weaning is fully complete. This is consistent with Smith et al., 2013.	Yes. The range of M_2 emergence overlaps the midpoint; however, M_2 emergence may occur prior to the midpoint.	If M1 ≤ 4 and $M_2 = 4$, then code for weaned. Otherwise, code for not weaned.
Pan paniscus	No? No data are available for M_1 emergence; therefore, this study relied on the emergence data for a maxillary M1 (see Table 3.1) as a proxy for M_1. M1 emergence is slightly after the midpoint. If M1 is scored a 1 or 2 then code for not weaned. If M1 is scored a 3 or 4, then code for weaned.	No. Since there are no emergence data for M_2 and the current data for M1 emergence nearly aligns with the midpoint, the coding for weaning status was based only on the M1.	If M1 is ≥ 3, then code for weaned. Otherwise, code for not weaned.

Pongo pygmaeus	No. M_1 emerges prior to the midpoint. If M_1 is scored a 1,2,3,or 4, then code for weaned.	Possibly? Data for M_2 emergence are lacking. Smith et al. (1994) report M_2 emergence at ~5.0 years; however, they also cite M_1 emergence at ~ 3.5 years. Kelley and Schwartz (2010) estimate M_1 emergence at ~4.6 years and so the Smith et al. (1994) M_1 emergence age is unlikely, but future work may find that 3.5 years of age is within the range of normal variation for M_1 emergence in *P. pygmaeus*. I noted that for a once captive *P. abelii* specimen curated in Zurich, the museum records documented an age of 6.5 years for this individual; however, the M_2 had not yet emerged. Little is known about the intergeneric dental developmental variation between the *Pongo* species. Beynon et al. (1991) analyzed the dental development for a *P. pygmaeus* individual, and they reported M_2 crown completion at ~ 5 years, but Beynon et al. (1991) did not provide an estimate for M_2 emergence. If the midpoint for age at weaning is at ~ 6 years of age, then perhaps, weaning coincides with M_2 emergence in *P. pygmaeus*.	If $M_1 \leq 4$ and $M_2 \geq 3$, then code for weaned. Otherwise, code for not weaned.

However, compared to the *P. abelii* individual, M_2 emergence would occur after the midpoint. Therefore, since the cessation of suckling is likely to occur after M_1 emergence, the weaning status had to be based on the M_2 (i.e., $M_1 = 1$ or 2 or 3 or 4 could be from either a not weaned or weaned individual). Since it is possible that M_2 emergence closely coincides with weaning in *P. abelii*, and *P. pygmaeus* weans, on average, earlier than *P. abelii*, I decided to code an individual as not weaned if the $M_2 \leq 2$ and weaned if the $M_2 \geq 3$.

Table 3.4. Sample size based on assigned weaning status

Taxa	Not Weaned	Weaned	Total
G. g. gorilla	67	18	85
P. paniscus	10	20	30
P. t. schweinfurthii	39	4	43
P. pygmaeus	27	14	41

Table 3.5. Descriptive statistics for unworn dp_4s

	N	Slope	Angularity	RFI	OPCRs	PDE
		Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)
G. g. gorilla	16	43.49 (2.40)	87.64 (0.26)	166.23 (6.15)	56.06 (4.59)	0.52 (0.77)
P. paniscus	9	42.30 (2.92)	88.29 (0.23)	162.40 (7.68)	57.49 (6.77)	0.87 (1.28)
P. t. schweinfurthii	14	40.28 (2.75)	87.96 (0.33)	154.35 (9.46)	53.42 (5.20)	0.78 (0.53)
P. pygmaeus	14	37.69 (1.89)	88.03 (0.34)	147.94 (7.76)	61.22 (6.10)	0.61 (0.16)

Table 3.6. Tests for homogeneity of variances for unworn dp_4 analyses

Occlusal Measurement	Levene Statistic	df1, df2	*p*-value
dp_4 Slope	1.141	3, 49	0.342
dp_4 Angularity	1.116	3, 49	0.352
dp_4 RFI	1.720	3, 49	0.175
dp_4 OPCR	0.872	3, 49	0.462
dp_4 PDE	1.138	3, 49	0.343

Table 3.7. One-way ANOVA results for unworn dp4s

Occlusal Measurement		SS	df	MS	F	*p*-value
dp_4 Slope	Between Groups	274.564	3	91.521	14.984	< 0.001*
	Within Groups	299.285	49	6.108		
	Total	573.849	52			
dp_4 Angularity	Between Groups	2.628	3	0.876	9.912	< 0.001*
	Within Groups	4.331	49	0.088		
	Total	6.960	52			
dp_4 RFI	Between Groups	2853.371	3	951.124	15.571	< 0.001*
	Within Groups	2992.975	49	61.081		
	Total	5846.346	52			
dp_4 OPCR	Between Groups	445.302	3	148.434	4.791	0.005*
	Within Groups	1518.195	49	30.984		
	Total	1963.497	52			
dp_4 PDE	Between Groups	2.377	3	0.792	0.499	0.684
	Within Groups	77.736	49	1.586		
	Total	80.113	52			

* $p \leq 0.05$

Table 3.8. Unworn dp_4 post hoc test results

i	*j*	Slope	Angularity	RFI	OPCR	PDE
G. g. gorilla	*P. paniscus*	1.19	**-0.64**^{T,B}	3.84	-1.42	-0.35
	P. t. schweinfurthii	**3.20**^{T,B}	**-0.32**^{T,B}	**11.88**^{T,B}	2.64	-0.26
	P. pygmaeus	**5.80**^{T,B}	**-0.40**^{T,B}	**18.23**^{T,B}	-5.16	0.21
P. paniscus	*P. t. schweinfurthii*	2.02	0.32	8.04	4.07	0.09
	P. pygmaeus	**4.61**^{T}	0.25	**14.46**^{T,B}	-3.74	0.56
P. t. schweinfurthii	*P. pygmaeus*	**2.60**^{T}	-0.08	-6.14	**-7.80**^{T,B}	0.47

^{T}Tukey's honestly significant-difference ^{B}Bonferroni. Signficant results bolded.

Table 3.9. Descriptive statistics for the "Not Weaned" category (Raw values, not ranked values, are presented.)

Taxon	N	Slope Mean (Std. Dev)	Angularity Mean(Std. Dev)	RFI Mean (Std. Dev)	OPCRs Mean (Std. Dev)	PDE Mean (Std. Dev)
G. g. gorilla	67	41.12 (3.47)	87.32 (0.45)	160.43 (9.18)	42.44 (5.14)	2.61 (3.34)
P. paniscus	10	41.47 (3.40)	88.27 (0.22)	161.17 (8.21)	41.33 (5.50)	1.25 (1.70)
P. t. schweinfurthii	39	37.18 (4.69)	87.66 (0.75)	149.02 (9.35)	37.13 (5.43)	5.43 (12.33)
P. pygmaeus	27	36.78 (2.81)	87.88 (0.57)	146.21 (7.20)	44.57 (7.60)	0.82 (1.59)

Table 3.10. Descriptive statistics for the "Weaned" category (Raw values, not ranked values, are presented.)

Taxon	N	Slope	Angularity	RFI	OPCRs	PDE
		Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)	Mean (Std. Dev)
G. g. gorilla	18	33.39 (4.08)	86.15 (1.02)	146.44 (12.43)	40.85 (12.02)	19.44 (12.70)
P. paniscus	20*	35.45 (5.76)	87.27 (1.06)	150.11 (12.04)	34.76 (7.04)	17.89 (17.20)
P. t. schweinfurthii	4	30.36 (3.10)	86.78 (0.61)	137.64 (3.79)	33.17 (10.50)	29.78 (24.58)
P. pygmaeus	14	32.29 (2.09)	86.97 (0.65)	139.66 (5.55)	38.67 (5.26)	7.89 (6.36)

*There are only 19 individuals of *P. paniscus* for the PDE variable.

Table 3.11. Levene's test of equality of error variances for raw data MANOVA

Occlusal Measurement	F	df1, dp2	*p*-value
dp_4 Slope	3.486	7, 189	0.002*
dp_4 Angularity	3.995	7, 189	< 0.001*
dp_4 RFI	1.583	7, 189	0.143
dp_4 OPCR	2.364	7, 189	0.025*
dp_4 PDE	21.190	7, 189	0.001*

* $p \leq 0.05$

Table 3.12. Two-factor Ranked MANOVA results

Two-factor ranked MANOVA model	Pillai's trace	F	df	p-value
Taxon	0.767	12.848	15,561	< 0.001*
Weaning Status	0.372	21.964	5,185	< 0.001*
Taxon * Weaning Status	0.163	2.155	15,561	0.007*

*$p \leq 0.05$

Table 3.13. Univariate effects for species (based on ranked values)

Dependent Variable	df, df error	F	P-value	Species	Ranked Means	95% Confidence Interval	
						Lower Bound	Upper Bound
Ranked Slope	3, 189	10.411	0.000*	*G.g. gorilla*	95.698	84.017	107.379
				P. paniscus	113.066	95.876	130.255
				P. t. schweinfurthii	58.215	35.114	81.315
				P. pygmaeus	59.000	44.414	73.586
Ranked Angularity	3, 189	22.528	0.000*	*G.g. gorilla*	57.846	46.259	69.424
				P. paniscus	140.547	123.502	157.592
				P. t. schweinfurthii	87.910	65.004	110.816
				P. pygmaeus	103.409	88.946	117.872
Ranked RFI	3, 189	17.743	0.000*	*G.g. gorilla*	106.538	94.687	118.389
				P. paniscus	119.653	102.213	137.093
				P. t. schweinfurthii	54.865	31.429	78.302
				P. pygmaeus	51.912	37.114	66.710
Ranked OPCRs	3, 189	2.005	0.115	*G.g. gorilla*	105.321	90.932	119.710
				P. paniscus	103.655	82.481	124.830
				P. t. schweinfurthii	83.489	55.033	111.944
				P. pygmaeus	123.349	105.382	141.316
Ranked PDE	3, 189	4.667	0.004*	*G.g. gorilla*	128.402	116.711	140.093
				P. paniscus	108.337	91.133	125.541
				P. t. schweinfurthii	126.728	103.08	149.847
				P. pygmaeus	94.997	80.399	109.595

* $p \leq 0.05$

Table 3.14. Univariate effects for weaning status (based on ranked values)

Dependent Variable	df, df error	F	*p*-value	Weaning Status	Ranked Means	95% Confidence Interval	
						Lower Bound	Upper Bound
Ranked Slope	1,189	64.457	0.000*	Not Weaned	116.422	107.113	125.730
				Weaned	46.568	32.148	60.687
Ranked Angularity	1,189	74.576	0.000*	Not Weaned	134.680	125.450	143.910
				Weaned	60.174	45.876	74.472
Ranked RFI	1,189	37.899	0.000*	Not Weaned	110.414	100.970	119.858
				Weaned	56.070	41.440	70.700
Ranked OPCRs	1,189	0.500	0.480	Not Weaned	107.744	96.278	119.210
				Weaned	100.163	82.401	117.926
Ranked PDE	1,189	91.575	0.000*	Not Weaned	72.950	63.633	82.266
				Weaned	156.282	141.850	170.714

* $p \leq 0.05$

Table 3.15. Post hoc *Ranked MANOVA results (Mean Difference I-J) for taxonomic groups comparisons*

i	j	Slope	Angularity	RFI	OPCR	PDE
G. g. gorilla	*P. paniscus*	18.840	**-54.296**^{T,B}	15.39	-2.78	-15.66
	P.t.schweinfurthii	**33.227**^{T,B}	**-45.946**^{T,B}	**47.22**^{T,B}	14.22	15.66
	P. pygmaeus	**55.179**^{T,B}	**-42.390**^{T,B}	**69.90**^{T,B}	**-32.88**^{T,B}	21.69
P. paniscus	*P.t.schweinfurthii*	14.387	8.350	**31.83**^{T,B}	17.01	**31.31**^{T}
	P. pygmaeus	**36.340**^{T,B}	11.91	**54.51**^{T,B}	-30.10	**37.35**^{T}
P.t.schweinfurthii	*P. pygmaeus*	21.952	3.56	22.68	**-47.10**^{T,B}	6.035

^{T} Tukey's honestly significant-difference; ^{B}Bonferroni correction. Signficant results bolded.

Table 3.16. Post hoc *ranked MANOVA results (Mean Difference I-J) for weaning status comparisons (species-pooled).*

Dependent Variable	i	j	Mean Difference
Ranked Slope	Not Weaned	Weaned	**69.854**
Ranked Angularity	Not Weaned	Weaned	**74.506**
Ranked RFI	Not Weaned	Weaned	**54.344**
Ranked OPCRs	Not Weaned	Weaned	7.581
Ranked PDE	Not Weaned	Weaned	**-83.333**

Bonferroni correction applied. Signficant results bolded.

Table 3.17. T-tests ranked data (intraspecific compairsons between 'not weaned' vs. 'weaned' categories)

Taxa	Dependent Variable	df	t
G. g. gorilla	Ranked Slope	83	7.844*
	Ranked Angularity	83	5.635*
	Ranked RFI	83	5.784*
	Ranked OPCRs	83	-2.342
	Ranked PDE	83	-7.272*
P.t.schweinfurthii	Ranked Slope	41	2.835*
	Ranked Angularity	41	2.946*
	Ranked RFI	41	2.428*
	Ranked OPCRs	41	-0.166
	Ranked PDE	41	-3.303*
P. paniscus	Ranked Slope	28	3.165*
	Ranked Angularity	28	4.032*
	Ranked RFI	28	2.606
	Ranked OPCRs	28	1.333
	Ranked PDE	27	-4.395*
P. pygmaeus	Ranked Slope	39	5.088*
	Ranked Angularity	39	5.673*
	Ranked RFI	39	2.992*
	Ranked OPCRs	39	1.806
	Ranked PDE	39	-6.583*

* p-value ≤ 0.05

Table 3.18. Follow-up two-factor ranked MANOVA results. (Between-subject effects for interaction results are only reported when the overall interaction was significant)

Two-factor ranked MANOVA model				
G. gorilla and P. paniscus	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.539	24.804	5, 106	< 0.001*
Weaning Status	0.418	15.227	5, 106	< 0.001*
Taxon * Weaning Status (Overall)	0.133	3.241	5, 106	0.009*
Between-Subject Interaction Results		*F*	*df*	*p-value*
Taxon * Weaning Status (Ranked Slope)		1.059	1, 110	0.306
Taxon * Weaning Status (Ranked Angularity)		1.833	1, 110	0.179
Taxon * Weaning Status (Ranked RFI)		0.587	1, 110	0.445
Taxon * Weaning Status (Ranked OCPR)		6.630	1, 110	0.011*
Taxon * Weaning Status (Ranked PDE)		0.104	1, 110	0.748
G. gorilla and P. t. schweinfurthii	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.345	12.635	5,120	< 0.001*
Weaning Status	0.311	10.822	5,120	< 0.001*
Taxon * Weaning Status	0.040	1.000	5,120	0.421
G. gorilla and P. pygmaeus	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.604	35.701	5,117	< 0.001*
Weaning Status	0.509	24.282	5,117	< 0.001*
Taxon * Weaning Status	0.218	6.536	5,117	< 0.001*
Between-Subject Interaction Results		*F*	*df*	*p-value*
Taxon * Weaning Status (Ranked Slope)		5.895	1, 121	0.017*
Taxon * Weaning Status (Ranked Angularity)		3.060	1, 121	0.083
Taxon * Weaning Status (Ranked RFI)		4.194	1, 121	0.043*
Taxon * Weaning Status (Ranked OCPR)		8.757	1, 121	0.004*
Taxon * Weaning Status (Ranked PDE)		0.010	1, 121	0.922

P. paniscus and P. t. schweinfurthii	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.221	3.637	5,64	< 0.001*
Weaning Status	0.312	5.815	5,64	< 0.001*
Taxon * Weaning Status	0.026	0.347	5,64	0.882
P. paniscus and P. pygmaeus	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.506	12.479	5,61	< 0.001*
Weaning Status	0.506	12.488	5,61	< 0.001*
Taxon * Weaning Status	0.031	0.385	5,61	0.857
P.t.schweinfurthii and P. pygmaeus	*Pillai's trace*	*F*	*df*	*p-value*
Taxon	0.121	2.065	5,75	0.079
Weaning Status	0.353	8.168	5,75	< 0.001*
Taxon * Weaning Status	0.049	0.776	5,75	0.570

* $p \leq 0.05$

Table 3.19. Discriminant function analysis for 'not weaned' category

Test of Functions	Wilks' Lambda	Chi-Square	df	p-value
1 thru 3	0.215	209.755	15	< 0.001*
2 thru 3	0.726	43.774	8	< 0.001*
3	0.885	16.665	3	0.001*

* $p \leq 0.05$

Table 3.20. Standardized canonical discriminant function coefficients for 'not weaned' category

	Function		
	1	2	3
Ranked Slope	0.640	-0.601	-0.154
Ranked Angularity	-1.136	0.895	-0.124
Ranked RFI	0.6247	1.001	.404
Ranked OPCRs	-0.052	-0.268	0.905
Ranked PDE	0.164	0.673	-0.220

Table 3.21. Structure matrix for 'not weaned' category

	Function		
	1	2	3
Ranked Slope	0.338	0.517	0.361
Ranked Angularity	-0.419	0.661	0.336
Ranked RFI	0.440	0.642	0.412
Ranked OPCRs	-0.162	-0.089	0.940
Ranked PDE	0.141	0.078	-0.363

Table 3.22. Classification results for 'not weaned' category

	Successful Predicted Group Membership (%)			
	G. g. gorilla	*P. paniscus*	*P. t. schweinfurthii*	*P. pygmaeus*
G. g. gorilla	**91.0**	3.0	6.0	0.0
P. paniscus	10.0	**80.0**	10.0	0.0
P. t. schweinfurthii	7.7	15.4	**53.8**	23.1
P. pygmaeus	0.0	3.8	19.2	**76.9**

Table 3.23. Discriminant function analyses for 'weaned category'

Test of Functions	Wilks' Lambda	Chi-Square	df	p-value
1 thru 3	0.330	54.890	15	< 0.001*
2 thru 3	0.652	21.191	8	0.007*
3	0.918	4.217	3	0.239

* $p \leq 0.05$

Table 3.24. Standardized canonical discriminant function coefficients for 'weaned" category

	Function		
	1	2	3
Ranked Slope	-0.550	0.675	0.483
Ranked Angularity	1.766	0.265	0.528
Ranked RFI	-0.633	0.312	-1.036
Ranked OPCRs	-0.592	-0.241	-0.047
Ranked PDE	0.157	0.859	1.097

Table 3.25. Structure matrix for 'weaned" category

	Function		
	1	2	3
Ranked Slope	0.117	0.624	-0.640
Ranked Angularity	0.548	0.399	-0.557
Ranked RFI	-0.004	0.754	-0.631
Ranked OPCRs	-0.247	-0.131	-0.164
Ranked PDE	-0.329	0.240	.0858

Table 3.26. Classification results for 'weaned' category

	Successful Predicted Group Membership (%)			
	G. g. gorilla	*P. paniscus*	*P. t. schweinfurthii*	*P. pygmaeus*
G. g. gorilla	**83.3**	3.0	11.1	5.6
P. paniscus	15.8	**52.6**	15.8	15.8
P. t. schweinfurthii	0.0	0	**75.0**	25.0
P. pygmaeus	0.0	7.1	21.4	**71.4**

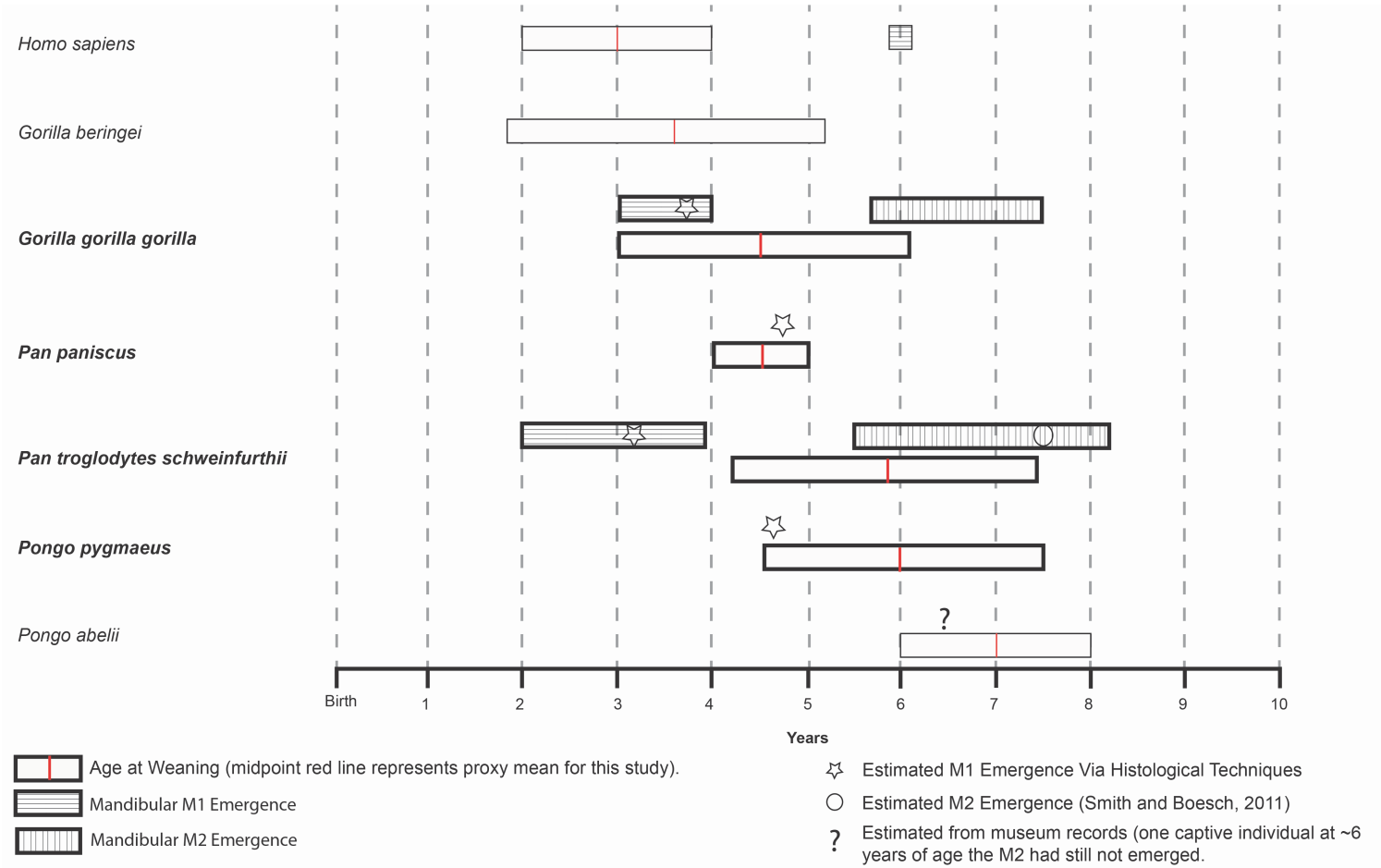


Figure 3.1. Summary of age at weaning, M1, and M2 data to create binary coding system to assign a weaning status (i.e., 'not weaned' vs. 'weaned') for each individual specimen. For references, see Table 3.1. See text for additional details. This study anazlyed dp_4s from the species in bold.

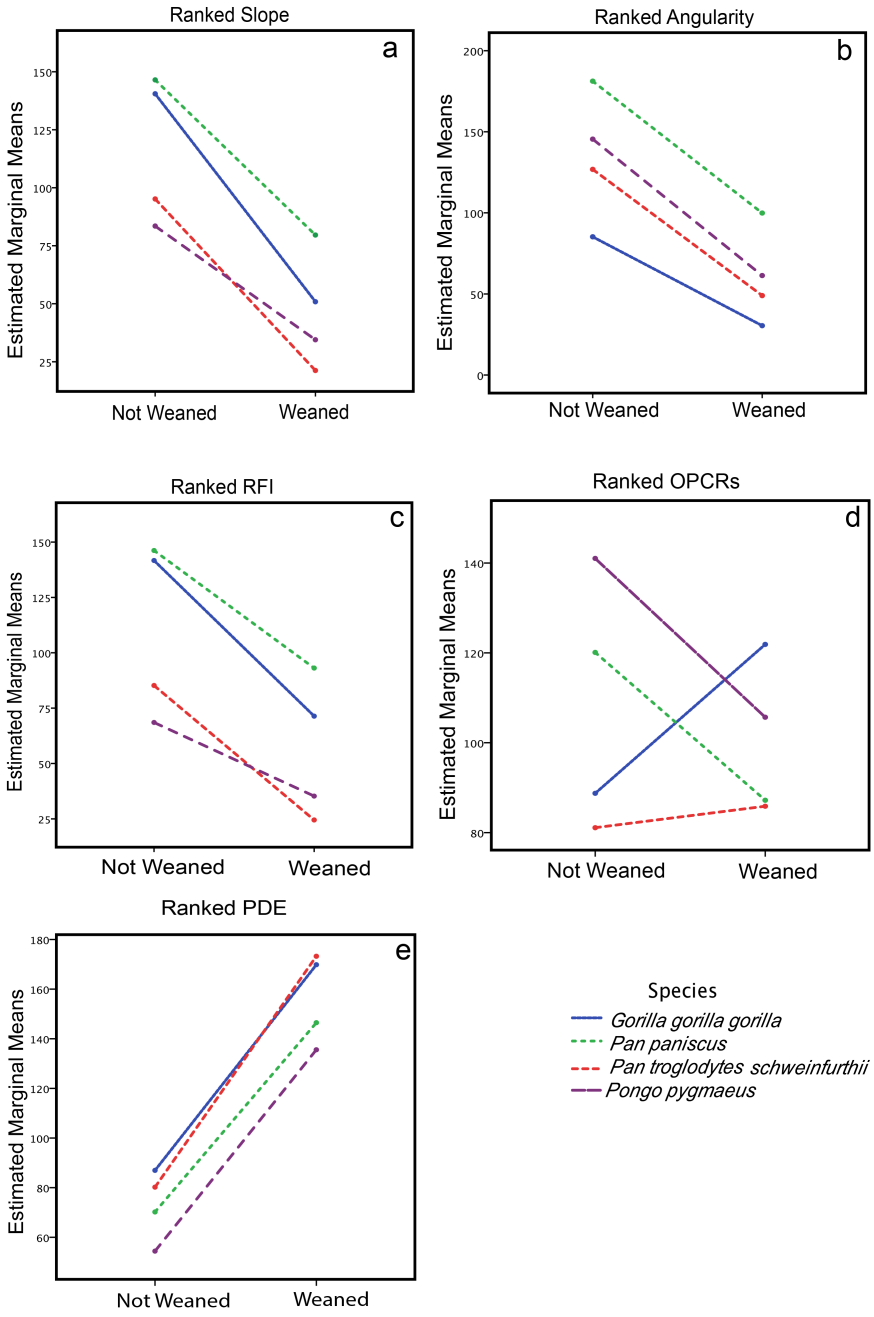


Figure 3.2. Interaction plots from ranked two-way MANOVA

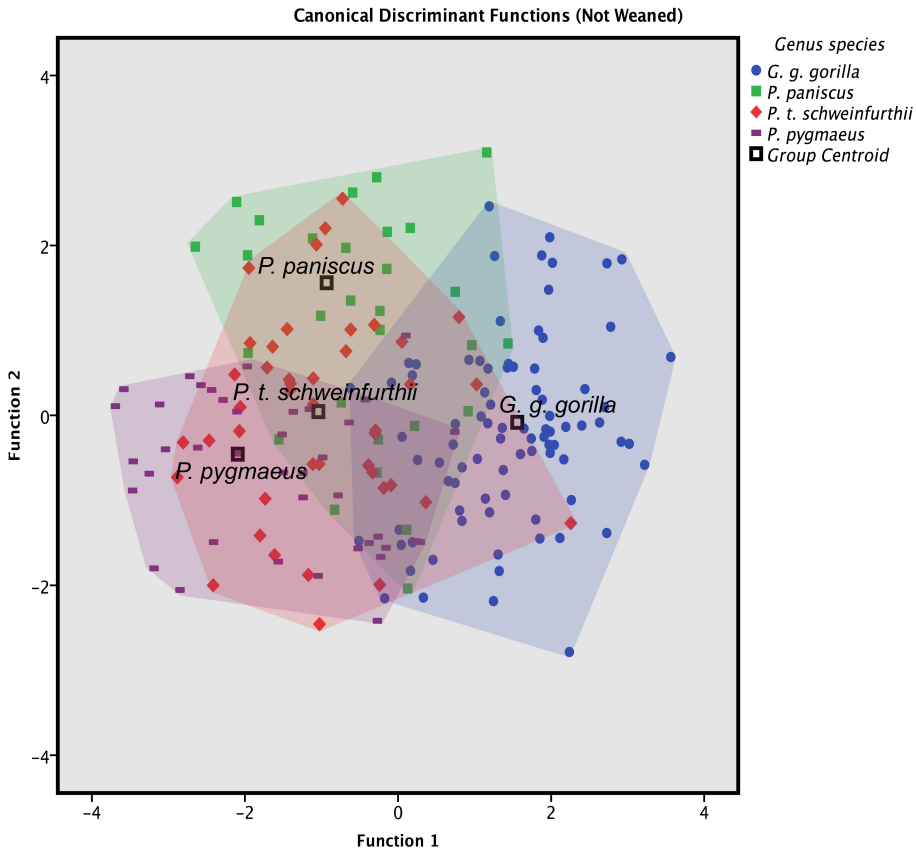


Figure 3.3. Discriminant function analysis comparing species in the 'not weaned' category

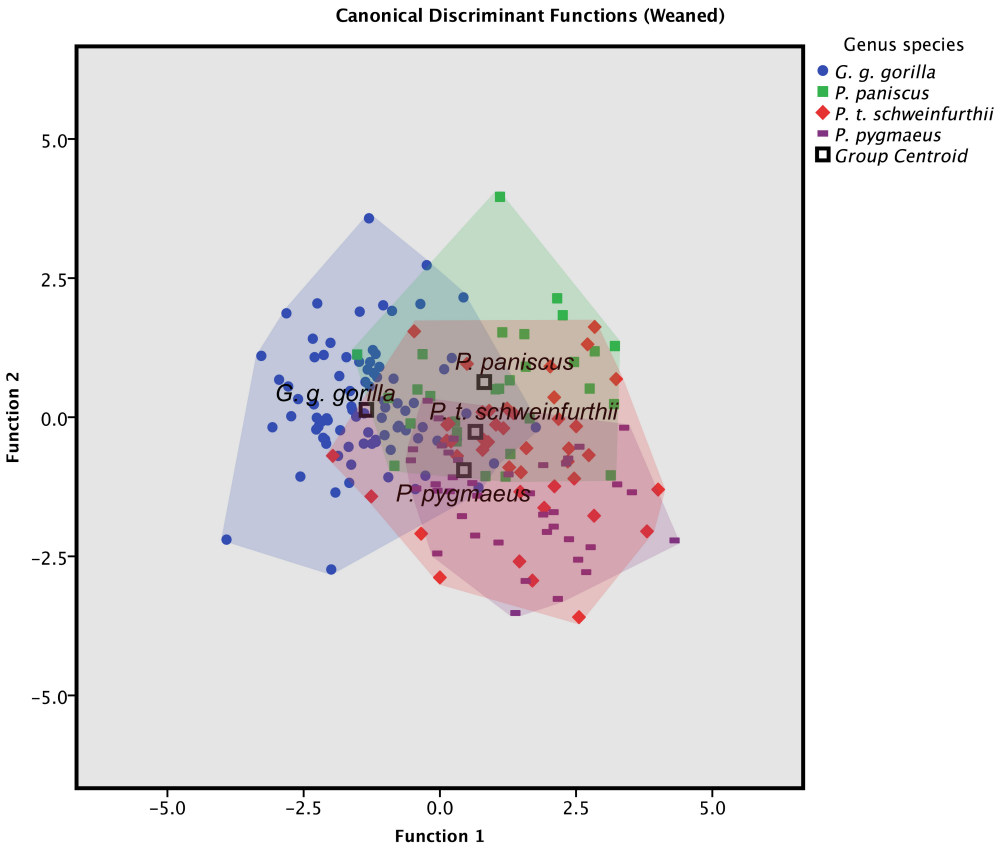


Figure 3.4. Discriminant function analysis comparing species in the 'weaned' category

CHAPTER 4

BODY SIZE, BRAIN SIZE, MOLAR SIZE, AND THE PACE OF DENTAL DEVELOPMENT WITHIN THE INDRIID-PALAEOPROPITHECID CLADE

Abstract

Objectives: Madagascar's variable environment dictates the reproductive ecology of many lemur species; therefore, along with brain size, but not body size, ecological and life history variables (e.g., age at weaning) are good correlates of the pace of dental development in several Malagasy lemurs. In comparison to other lemurs, the species studied thus far in the indriid-palaeopropithecid clade exhibit an extreme pattern where dental development is incredibly fast but the pace of somatic development is very slow. To attain such a fast dental developmental schedule, this clade has diminutive deciduous premolars that are shed very quickly. The objective of this study is fourfold. First, new dental developmental data are presented for *Indri indri* and *Avahi laniger* to complement previous research on this clade. Second, tests for associations between the rate of molar development and brain and body size are conducted to assess whether brain or body size are good predictors of the pace of dental development within this clade. Third, since the timing of a molar's initiation and its final size reflect a linear developmental cascade among the primary postcanine dentition (i.e., deciduous premolars and permanent molars), this study also tests whether extant and extinct lemurs, including species outside the indriid-palaeopropithecid clade, adhered to predictions of the inhibitory cascade (IC) model. Finally, since molar size is the phenotypic manifestation of the developmental interactions that occur within the

primary postcanine dentition, associations are assessed among molar size, body and brain size, and two life history variables (i.e., gestation length and age at weaning) in several extant lemurs.

Material and Methods: Using histological techniques, the rate of molar development was quantified in *I. indri* (n=1) and *A. laniger* (n=1). Body size, brain size, gestation length, age at weaning data, and molar area were collected from the literature. Correlation tests (i.e., Pearson's r and Spearman's rho) were conducted to test whether significant relationships exist between size variables and life history variables. Reduced major axis regressions were used to test whether lemurs adhere to the predictions of the IC model.

Results: As expected, *I. indri* and *A. laniger* exhibit extremely fast dental developmental schedules. The smallest bodied indriid, *Avahi*, and the larger bodied *Palaeopropithecus* both have extremely early M1 development (i.e., 96.6% and 84.6%, respectively, of the crown is formed *in utero*). In *A. laniger* the initiation of the M_1 and M_2 are nearly coincident in time, and in all remaining members of the indriid-palaeopropthecid clade for which there are data available, the proportion of M2 enamel that develops *in utero* is relatively consistent. Correlation tests among the rate of molar development, body size, and brain size revealed no significant relationships, suggesting that body and brain size are not good predictors for the fast pace of dental development observed this clade. The IC model was tested using maxillary (22 species) and mandibular (16 species) molar triplets (i.e., M1-M2-M3) for extant and extinct species of lemurs. In general, lemurs adhered to the mathematical predictions of the IC model, but there were several exceptions. The results of the correlation tests, which were only conducted on extant

species, revealed that body size and molar areas are significantly correlated. Brain size is also correlated with molar size. Age at weaning was most strongly associated with the size of the mandibular, not maxillary, molars. Gestation length was not significantly correlated with molar size. Of all the molars, the M2 size yielded the highest correlations with body size, brain size, and age at weaning.

Discussion: Given the new dental developmental data for the indriids, the reconstructed gestation length of the extinct large-bodied *P. ingens* was reassessed. The incorporation of the IC model within a life history context provides evidence that size of the M_2, and by extension the timing of M_2 emergence, may be an additional target of selection to ensure dental precocity and availability of an adult-like dentition at weaning. Future research directions are discussed.

Introduction

Between 60-50 million years ago early primates rafted to Madagascar, where they diversified rapidly and eventually occupied several niches on the island (Poux et al., 2005; Ali and Huber, 2010). Approximately 4000-5000 years ago, humans arrived on the island and disturbed Madagascar's ecosystem, which resulted in mass extinctions across the island (e.g., Perez et al., 2005; Douglass and Zinke, 2015; Burns et al., 2016). Larger fauna (i.e., >10 kg) were particularly at risk, including the largest lemurs, and went extinct about 500 years ago (e.g., Burney et al., 2004; Crowley, 2010). The extinction of the large-bodied lemurs continues to affect the ecological balance of the island, as some large-bodied lemurs were key seed-dispersers and are no longer present to help rejuvenate the forests (Godfrey et al., 2008; Winchester et al., 2014). Human

disturbance of the forests continue to place the remaining species on the threshold of extinction (e.g., Wright et al., 2005; Schwitzer et al., 2014). The large-bodied lemurs were just as diverse as the extant large-bodied primates elsewhere in the world, and studies of subfossil lemurs provide a number of lessons about primate adaptation and evolution (e.g., Godfrey et al., 1997; Godfrey et al., 2002; Godfrey and Jungers, 2003; Godfrey et al., 2005; Godfrey et al., 2008; Jungers et al., 2008; Polk et al., 2010; Scott et al., 2009; Godfrey et al., 2011; Scott, 2012; Godfrey et al., 2015; Kistler et al., 2015). One of these lessons concerns the relationships among brain size, body size, dental growth, and life history profiles.

Primates have relatively larger brains, slower metabolic rates, and slower life history schedules than other mammals (e.g., Charnov and Berrigan, 1993; Navarrete et al., 2011; Pontzer et al., 2014). The study of variation in these traits provides important opportunities to assess how primates respond to socioecological challenges, such as obtaining preferred resources, navigating complex social relationships associated with group-living, and mitigating mortality risks when living in unpredictable environments. Janson and van Schaik (1993) proposed an ecological risk aversion hypothesis that seemed to account for differences in growth rates of folivorous and frugivorous primates. Presumably, since there is a greater abundance of food resources for folivores than frugivores, frugivorous primates should grow their brains, bodies, and teeth at slower rates than folivorous primates, as slower growth rates would mitigate starvation risks, conserve energy, and decrease juvenile mortality (Janson and van Schaik, 1993).

Subsequent research on monkeys and apes supported Janson and van Schaik's hypothesis, as faster body growth rates tend to coincide with faster dental developmental

schedules, and folivores tended to grow faster than frugivores (e.g., Leigh and Shea, 1996; Dirks, 2003). Godfrey et al. (2002) demonstrated that the basic premises of the Janson-van Schaik hypothesis did not hold in lemurs; frugivorous lemurs tend to have faster rates of body growth. In addition, there is a disassociation between body and dental growth. While folivorous lemurs have slower body growth rates, their dental development can be extremely fast, much faster than frugivorous lemurs (e.g., Godfrey et al., 2005). This dissociation partially explains why other somatic and dental developmental predictions found to hold for monkeys and apes do not hold for the lemurs (e.g., cf. Smith, 1992 and Godfrey et al., 2005).

Decades of research on primates have found that brain size, and to a lesser degree body size, is a good predictor for the pace of growth and development (e.g., Sacher, 1959; Martin 1981; Isler and van Schaik, 2009). Brain size is also a good predictor for life history variables, particularly those variables that are associated with both maternal energetic expenditures and energetic requirements of offspring (e.g., litter size, gestation and lactation length, and reproductive lifespan) (e.g., Weisbecker and Goswami, 2010; Isler and van Schaik, 2012). While brain size, rather than body size, is a better predictor of reproductive rates in lemurs, brain size is only moderately associated with body size and pace of dental development (e.g., Godfrey et al., 2003; Schwartz et al., 2005; MacLean et al., 2009; Catlett et al. 2010). Rather than brain or body size, ecological and dietary factors seem to explain the variation observed in the growth and development of Malagasy lemurs (e.g., Eaglen, 1985; Godfrey et al., 2004; Hogg et al., 2015). Selection seems to target traits (such as dental precocity at weaning and dp4/M1 size ratios) that may influence when adult-like food processing skills and

foraging independence are acquired (Godfrey et al. 2002; Godfrey et al. 2003). A consideration of Madagascar's environment helps explain why dietary and ecological factors are better predictors than brain and body size, per se.

Madagascar's modern environment is paradoxically both predictable and unpredictable. Madagascar annually cycles through a predictable wet and dry period (e.g., Wright, 1999; Dewar and Richard, 2007). While most lemurs are seasonal breeders, with species having nonsynchronous breeding and birthing cycles, phenological observations revealed a synchronous weaning pattern across lemur species, regardless of body size, as nearly all lemurs wean at the same time, and this 'weaning season' coincides when fruits are most available (Wright, 1999; Wright et al., 2005). The aye-aye (*Daubentonia madagascariensis*) is the key exception; it is an extractive forager and less constrained to the synchronous weaning cycle (Sterling, 1994).

When tracked long-term (i.e., over multiple years), Madagascar's environment is quite unpredictable due to irregularities in precipitation levels, which inhibit the production of leaves, or occasional cyclones, which, initially, are a destructive force on the forests and displace the fauna (Ganzhorn, 1995; Dewar and Richard, 2007). Recent paleoclimate simulations discovered that when primates first arrived on the island (~60-50 mya), Madagascar's environment was dry, but more stable (e.g., less seasonal rainfall and fewer cyclones), which is very different from the more extreme seasonal conditions observed today (Ohba et al., 2016). Dewar and Richard (2007) hypothesized that Madagascar's unpredictable environment resulted in several Malagasy mammals evolving a bet-hedging reproductive strategy, a pattern primatologists have documented in other lemur species (Richard et al., 2002; Irwin, 2007; Godfrey and Rasoazanabary,

2012). Given Ohba et al's (2016) palaeoclimate study, if Dewar and Richard (2007) are correct that some of the unusual life histories that characterize modern lemurs (e.g., torpor, bet-hedging) evolved in response to more a unpredictable environment, then the evolution of these traits is likely a relatively recent phenomenon (i.e., perhaps during the Oligocene) (Kistler et al., 2015; Ohba et al., 2016).

Bet-hedging occurs when the target of selection is the *variance* in total reproductive output rather than the *mean* (e.g., Stearns, 1992; Richard et al., 2002; Olofsson et al. 2009). In other words, reproductive strategies evolve to maximize fitness by decreasing the variance of fecundity over the lifespan. On average, primates produce one or, at most, two offspring at a time (Fleagle, 2013). One way to decrease the variance in overall fecundity is to protract the length of the reproductive stage in an animal's life history profile by increasing the animal's lifespan, enabling an animal to reproduce less often per unit of time but in a variety of environmental conditions (Stearns, 1992). This would increase the probability of at least one offspring being born in 'good' environmental conditions (e.g., a lemur baby being born during a year when food resources are plentiful).

Within a particular environmental context, several factors (e.g., phylogenetic, functional, physiological) limit the number of options available to maximize the reproductive lifespan (Roff, 2002). In addition, there are number of ways to be a 'bet-hedger' (reviewed by Olofsson et al. 2009). For example, the evolution of cooperative breeding in humans is likely an example of a bet-hedging strategy (Rubenstein, 2011); as humans have relatively long lifespans that are devoted to decreasing the variance in overall fecundity by shortening the weaning period and utilizing allomothering

strategies (i.e., grandmothers) to raise grandchildren and other relatives (e.g., nieces and nephews) (Hawkes et al., 1998; Hrdy, 2009). Sifakas (i.e., *Propithecus* spp.) have been dubbed "bet-hedgers par excellence" (Richard et al. 2002:431), as females exhibit delayed age at first reproduction (e.g., *Propithecus verreauxi*'s age at first reproduction is ~5-6 years), slow skeletal development, but extended lifespans (~20 years) (Wright, 1999; Godfrey et al., 2004; Irwin, 2007). Therefore, to adapt to Madagascar's unpredictable environment, *Propithecus* and other indriids have evolved an exceptionally rapid dental developmental schedule so that weanlings are prepared for the weaning season (e.g., Godfrey et al., 2003; Godfrey et al., 2005). The rapid dental developmental schedule appears to characterize the entire indriid family, as well as its sister group, the now-extinct Palaeopropithecidae (Godfrey and Jungers, 2003; Orlando et al., 2008; Kistler et al.,

2015; Figure 4.1).

The Indriidae comprises three genera (*Avahi*, *Propithecus*, and *Indri*) and includes the largest extant lemurs. The average body masses range from 1.3 kg – 6.8 kg (Table 4.1, citations therein). The indriids' closely related, and all recently extinct cousins, Palaeopropithecidae, comprise four genera (*Mesopropithecus*, *Babakotia*, *Palaeopropithecus*, and *Archaeoindris*; Figure 4.1). The Palaeopropithecidae exhibited a wide range of body masses (11-161 kg), which included some of the largest primates that ever lived (Table 4.2, citations therein). Schwartz et al. (2002) and Catlett et al. (2010) utilized dental histology to estimate molar crown formation times (CFTs) in *Palaeopropithecus ingens* and *Mesopropithecus globiceps* and confirmed that these two palaeopropithecids also exhibited extremely rapid dental development. As an example, *P.*

ingens had an estimated body mass of ~41.5 kg, about the size of a female gorilla (Jungers et al., 2008; Fleagle, 2013). A gorilla first molar (M1) crown requires ~2.8 years to develop, while the *P. ingens* M1 required only 0.61 years (Schwartz et al., 2002; Kelley and Schwartz, 2010). For all members of the indriid-palaeopropithecid clade for whom the pace of somatic growth and that of dental development have been studied, this clade exhibits a characteristic pattern: dental development is fast while somatic growth is slow (e.g., Godfrey et al., 2001; Godfrey et al., 2002; Schwartz et al., 2002; Godfrey et al., 2005).

The first objective of this paper is to contribute new dental developmental data using histological methods for *Indri indri* and *Avahi laniger*. Prior to this study, precise chronologies of dental development only existed for one indriid, *Propithecus verreauxi* (Schwartz et al., 2005). The addition of *I. indri* and *A. laniger* will provide at least one representative species for all genera in this clade (Figure 4.1). A second objective of this study is to compare these new data with previously published dental growth chronologies of *P. ingens* (Schwartz et al., 2002) and *M. globiceps* (Catlett et al., 2010) and to test for associations among molar formation times, brain size, and body size within the indriid- palaeopropithecid clade. Comparisons of prenatal CFTs are of particular interest because the amount of prenatal M1 development is key to helping reconstruct important life history traits, such as gestation length and interbirth interval, in extinct lemurs (Schwartz et al. 2002; Godfrey et al., 2006; Catlett et al., 2010).

This study also has a third objective: to assess another aspect of dental development, via the application of the IC model, and life history variables. In order to achieve such rapid dental development, both the indriids and palaeopropithecids have

sacrificed the size of their deciduous teeth (Godfrey et al., 2002). Dental development is so rapid that the deciduous teeth are essentially vestigial; they are diminutive in size and shed extremely early (e.g., Godfrey et al., 2002; Godfrey et al. 2003). For example, *A. laniger* neonates have all the deciduous dentition erupted and the permanent dentition has fully emerged by ~2.5-3.0 months of age (Godfrey et al., 2005). In some primates, like the great apes, the deciduous dentition functions for years and is an important component of the masticatory apparatus (Chapters 2 and 3). In contrast, the deciduous dentition in indriids is shed quickly to have a full adult dentition in place for the 'weaning season.' Within the context of dental development, a key consideration is the potential influence an accelerated deciduous developmental schedule may have on subsequent molar development in indriids, palaeopropithecids and lemurs in general.

Kavanagh et al. (2007) discovered the IC model, which predicts that the ratio of activators/inhibitors during the development of the anteriormost mandibular molar (i.e., M_1) will dictate the size and timing of initiation of subsequently developing molars (i.e., M_2 and M_3), creating a developmental cascade moving distally along the dental lamina. Kavanagh et al. (2007) generated a set of mathematical predictions, viz., that the maximum rectangular size ratios of M_2/M_1 and M_3/M_1 would have a linear relationship, specifically with a slope of 2.0 and y-intercept of -1.0. In addition, the middle tooth (i.e., M_2) should comprise 33% of the total molar row area. Daly and Catlett (2014) validated this model using the primary postcanine teeth (dp_3, dp4, and M_1) in platyrrhines, catarrhines, and hominins, and in doing so provided a developmental explanation as to why tooth size increases linearly from dp_3 to dp_4 to

M_1. The inclusion of the deciduous dentition showed how the development of the deciduous premolars could influence the development of the other postcanine primary teeth (i.e., molars).

The inclusion of the total primary postcanine row (sometimes ≥ 5 tooth positions) extends the original bivariate prediction comparing M_2/M_1 and M_3/M_1 into 3 dimensions (Evans et al., 2016). In addition, it has been observed that one of the teeth in the primary postcanine tooth row is the largest in the row, which seemingly disrupts the linear pattern. For example, for a large proportion of the modern human population, the M_1 is the largest tooth resulting in the following size pattern: dp3 < dp4 < M1 > M2 >M3. Hence, for modern humans, the linearity of the triplets dp3-dp4-M1 and M1-M2-M3 holds, but not for the dp4-M1-M2 triplet. The explanation for why the linear pattern does not hold for the dp4, M1, and M2 relates to the possible presence of a developmental shift. For example, the position of the largest tooth (e.g., M1) probably indicates a reversal, or a developmental shift, in the activator/inhibitor molecule ratio that influences the size (and possibly timing of initiation) of subsequently developing posterior teeth (Kavanagh et al. 2007; Evans et al., 2016). An important aside is that the predicted linearity among the various combinations of triplets are based on population means, not individuals, as specific individual developmental phenomenon (e.g., growth disturbances) within individuals may disrupt the expected linear size pattern (e.g., Daly et al., 2015; Evans et al., 2016).

Järvinen et al. (2008) partially explain the developmental connection between the deciduous teeth and molars. Using experimental data from tree shrews, they report that the earlier a permanent tooth initiates, the smaller the deciduous teeth; therefore, “any

selective factor favoring earlier development of permanent teeth [such as in the indriids] should automatically result in smaller deciduous teeth" (485:2008). Indeed, Godfrey et al. (2003) report that the size ratio between dp4/M1 (either maxillary or mandibular) predicts dental precocity at weaning across haplorhines and strepsirrhines, where species with relatively smaller dp4s compared to the M1s (i.e., *A. laniger)* are the most dentally precocious at weaning. Given the above discussion of Madagascar's environmental influence on lemur life history profiles, selection for dental precocity at weaning should influence the pace of dental development, such as early initiation of the molars (e.g., Godfrey et al., 2003; Järvinen et al. 2008). Therefore, the primary postcanine dentition in lemurs should adhere to the predictions outlined by the IC model. The expectation is that molars initiating and growing *in utero* are less likely to be disturbed by external, environmental perturbations that could affect the developmental controls of the IC model. Therefore, using published data on molar area, the third objective of this study is test whether the IC model holds for the molar triplet (i.e., M1-M2-M3) in lemurs. Although, the original IC study only focused on the mandibular primary postcanine dentition (Kavanagh et al., 2007), the maxillary primary postcanine dentition is considered as well, as there is no *a priori* reason at this time to assume that the maxillary primary postcanine dentition is not subject to the same developmental cascade mechanism. Due to the lack of available published data, the deciduous dentition is not included at this time; therefore, only the molars are considered.

Depending upon the taxonomic level, there is a long recognized relationship between molar area and other important ecological, dietary, and life history variables (e.g., body size, age at weaning, facial size) (e.g., Gingerich et al., 1982; Godfrey et al.,

2001; Copes and Schwartz, 2010; Scott, 2012). Given the expectation that the IC influences molar size and initiation, molar area can act as a proxy for dental development, which is useful since detailed dental developmental data for many lemur species are currently unpublished (e.g., Godfrey et al., 2006; Kavanagh et al., 2007; Evans et al., 2016). Since dietary and ecological factors seem to explain a greater proportion of the developmental variation in lemurs more reliably than body size or brain size, associations with brain size, body size, gestation length, and age at weaning among molar areas for each molar position are worth examining. This is the final objective of this paper. An exploration of molar areas, within the context of dental development (i.e., molar CFTs and the IC model), may provide a useful framework to explore life histories in lemurs, and, perhaps, other primates as well.

Hypotheses

The first objective of this chapter is to present new data on the molar CFTs of *I. indri* and *A. laniger*. Given previous research, it is expected that these two indriids will exhibit accelerated molar development (e.g., Godfrey et al., 2005). The second objective of this paper is to compare these new data with previously published molar chronologies for *P. verreauxi*, as well as with two closely related, but extinct species, *P. ingens* and *M. globiceps* and to assess if body size or brain size is more associated with aspects of molar formation times (e.g., prenatal CFT). Previous research suggests that brain size is a better predictor compared to body size for various aspects of lemur molar development and life history variables (e.g., age at weaning, reproductive rates); therefore, it is predicted that brain size, rather than body size, will be a better correlate

with molar CFTs (e.g., Schwartz et al., 2005). The third objective of this study is to test whether the IC model holds for lemurs. Given that this developmental model holds reasonably well across a number of mammalian taxa (e.g., Polly, 2007; Renvoisé et al., 2009; Wilson et al., 2012; Asahara, 2013; Bernal et al., 2013; Halliday and Goswami, 2013; Schroer and Wood, 2015; Evans et al., 2016), it is expected that it should also hold for the lemurs. Finally, the fourth goal is to assess the strength of associations among molar area, brain size, body size, gestation length, and age at weaning, as this will unite the developmental data garnered from molar size (i.e., an application of the IC model) with life history data. In primates, brain size, body size, gestation length, litter size, and territoriality have a strong phylogenetic signal (Kamilar and Cooper, 2013). Therefore, it is expected that molar areas will be significantly correlated with body size, brain size, gestation length, and age at weaning, four variables strongly correlated in extant lemur species.

Material and Methods

Sample of Tooth Sections

The maxillary molars used in this study were from a wild *I. indri* specimen that was dentally an adult; however, the dental wear on this specimen was so minimal that results should not be affected by wear. The *A. laniger* specimen used in this study was a juvenile killed by a raptor from a natural population under observation for behavioral studies in the Manombo Reserve, Madagascar. This individual was ~2.5 months old when it died. The mandibular third molar was missing from the specimen (due to postmortem loss) and so this analysis is based on the M_1 and M_2 and the M^3. Godfrey et al. (2005) published a photograph of the mandible for this particular individual.

While the mandibular teeth usually precede the development of the maxillary molars (e.g., Nanci, 2013), the dental development in the indriids is so fast that any difference between the mandibular and maxillary molars is likely negligible.

Histological Preparation and Analyses

Using standard histological techniques (e.g., Reid et al., 1998; Schwartz et al., 2005), molar chronologies were reconstructed for *I. indri* and *A. laniger*. Prior to sectioning, dental casts of the molar rows were prepared. Specimens were photographed and x-rayed. Each molar was extracted and then embedded in an epoxy resin block prior to being sectioned with a diamond-wafering blade saw (Buehler™ Isomet 5000). Longitudinal thin sections (~150μm in width) were taken from each molar[1] through the mesial and distal cusp tips to minimize section obliquity (Smith et al., 2006). After being mounted to a slide using an epoxy resin, the section was polished on a lapping machine until a thickness of ~80-100μm. Sections were analyzed and photographed using standard transmitted polarized light.[1]To reconstruct the molar chronologies, long- and short-period lines, found in both the enamel and dentine, were counted, and accentuated lines were cross-matched among the different molar positions (e.g., Schwartz et al., 2005; Schwartz and Dean, 2008). As a tooth develops, ameloblasts secrete proteins (enamelin and amelogenin) that mineralize and form the enamel; an analogous process occurs with odontoblasts, which secrete a collagenous matrix of predentine that mineralizes to form

[1] Ms. Pam Walton prepared the *A. laniger* sections at the Hard Tissue Laboratory in Newcastle-upon-Tyne, England. Dr. Patrick Mahoney prepared the *I. indri* sections at the Dental Anthropology Laboratory at Arizona State University. The author analyzed the sections.

dentine (e.g., Nanci, 2003). Extensive research has demonstrated that during the secretion of the enamel or dentine matrix, there are regular 24-hour fluctuations in the deposit of the matrix; these fluctuations leave a distinct line when viewed under a microscope. Depending on the dental tissue (i.e., enamel or dentine), these lines are called cross-striations, short-period lines, daily lines, or Von Ebner's lines (e.g., Kawasaki et al., 1977; Molnar, 1981; Bromage, 1991; Dean, 1993; Reid and Ferrell, 2006; Smith, 2006; Smith et al., 2006; Antoine et al., 2009).

In addition to these daily lines, longer periodic lines are also visible in the microstructures of teeth. The longer periodic lines also represent regular and predictable oscillations, but the timing of these oscillations depends on an individual's biorhythm (e.g., Bromage et al., 2009; Hogg et al., 2015). These long-period lines bracket the daily lines, and the same number of daily lines consistently appears between adjacent long period lines within an individual (reviewed by Smith, 2006). Long-period lines in enamel are called striae of Retzius, with the number of daily lines deposited between two adjacent striae called the periodicity, or, the Retzius period (Hogg et al., 2015). Dentine exhibits a similar pattern of long- period and short-period lines, called Andresen and von Ebner's lines, respectively. As for enamel, the periodicity of dentine lines remains the same, and identical to that for enamel, within the same individual (e.g., Dean, 1993; Dean et al., 1993; Dean, 1995). While each individual has a periodicity, which reflects that individual's biorhythm, there is a wide range of periodicities in primates (e.g., Hogg et al., 2015).

Since the periodicity records time, it is possible to calculate how long it took a tooth crown to grow. For example, a periodicity of 2 indicates that it took 2 days

(i.e., ~48 hours) to deposit that amount of either enamel or dentine matrix. While the daily lines capture information about time, the lengths of the cross-striations provide information about the rate of enamel or dentine matrix secretion. In the case of enamel, the amount of enamel matrix may vary from as little as ~1.0 μm/day to nearly ~7.4μm/day (Hogg and Walker, 2011; reviewed in Hogg et al., 2015). While lemurs tend to exhibit some of the fastest daily secretion rates, high daily secretion rates have been observed in humans as well (e.g., Mahoney, 2011).

Another important marker embedded within a tooth's microstructure is the neonatal line. The neonatal line results from the process of birth. The neonatal line is an important demarcation of the proportion of enamel that developed prenatally versus postnatally. Subsequent pronounced lines or enamel defects may indicate growth disturbances and may signify a period of illness or starvation (e.g., Goodman and Rose, 1990; FitzGerald et al., 2006; Guatelli-Steinberg and Benderlioglu, 2006). In primates with longer dental developmental schedules, the neonatal line is only visible in the cuspal enamel of teeth that initiated *in utero* (e.g., *Hadropithecus*, modern humans); however, the extremely early tooth initiation and rapid development of some lemur teeth will cause the neonatal line to appear in the lateral enamel. The neonatal and accentuated lines are used to cross-match different tooth positions to chart the dental growth chronology, which in this study is the chronology for the molar row (Schwartz and Dean, 2008).

In the study of lemurs, particular the subfossil lemurs, palaeobiologists are especially interested in the proportion of enamel that developed *in utero*, as this enables a reconstruction of gestation length. Teeth do not begin forming until the very end of, or

slightly after the onset of, the first trimester (Schwartz et al., 2002; Schwartz et al., 2005), and gestation length exhibits a strong phylogenetic signal (Kamilar and Cooper, 2013). Therefore, in closely related species, the proportion of enamel that developed *in utero* can be used as a model to estimate gestation lengths in the extinct lemur species (e.g., Schwartz et al., 2002; Godfrey et al. 2006).

Ideally, dental growth data should be collected from each individual cusp to calculate the total CFT. In this study, it was not possible to calculate the time it took each cusp to develop because not . Therefore, the CFTs presented in this study are estimates based on the protocone and protoconid cusps, which are usually the earliest initiating cusps that also exhibit the thickest enamel (Nanci, 2003; Schwartz, 2000); therefore, these cusps are good proxies for the total CFT as they capture nearly all of the crown growth period.

Data from Literature

Molar CFT data for *P. verreauxi*, *M. globiceps*, and *P. ingens* were collected from the literature (Schwartz et al., 2002; Schwartz et al., 2005; Catlett et al., 2010). Available data for body mass, brain size, gestation length, and age weaning were collected from the literature for extant and extinct lemur species (Tables 4.1 and 4.2, citations therein).

Rectangular areas for each molar position (i.e., M1, M2, and M3) were collected for both the maxillary and mandibular dentition (Tables 4.3 and 4.4, citations therein). For both mandibular and maxillary molars, areas were calculated as the maximum mesiodistal length × maximum buccolingual (or buccopalatal) width.

Analytical Methods

To assess associations of brain size and body size with aspects of molar CFTs within the indriid-palaeopropithcid clade, correlation matrices reporting Pearson's correlation coefficients (r) and its nonparametric equivalent, Spearman's rho, were calculated in SPSS v. 23. Due to small samples and violations of normality, data were logged. The aspects of M1 and M2 development considered were total CFT, prenatal CFT (i.e., the proportion of the crown that developed *in utero*), and postnatal CFT. Only prenatal M3 CFT was considered, but not total M3 CFT, as these data were not available for all members of the indriid-palaeopropithcid clade. For this analysis, no distinction was made between mandibular and maxillary molars due to limited sample sizes.

To test whether the IC model holds for lemurs, standard statistical protocols for this method (Kavanagh et al., 2007) were implemented (i.e., data were not logged and were analyzed with reduced major axis regressions using the smatr R-Package) (Warton et al., 2012; Smith, 2009). Maxillary and mandibular molar areas were analyzed separately. Tests were conducted to assess whether the slope or y-intercept was significantly different from 2.0 or -1.0, respectively, using the slope.test and elev.test functions in the smatr package (Warton et al., 2012). In addition, a morphospace based on Polly (2007) was generated in RStudio using ggplot2 (Wickham, 2009) to compare the predicted linear pattern (i.e., slope = 2, y-intercept=-1) of metameric molar size variation among different lemur taxa. Finally, based on the methods presented in Evans et al. (2016), the presence of any linear relationships (i.e.,

not specifically a slope=2, y- intercept=-1) in the mandibular or maxillary 'M1-M2-M3' triplet were tested for each individual species using RStudio.

Finally, Pearson's r and Spearman's rho were used to detect significant associations among brain size, body size, gestation length, and age at weaning with molar area for each molar position (i.e., M^1, M^2, M^3, M_1, M_2, and M_3). To account for small sample sizes and violations of normality, data were logged for this analysis. Since molar developmental data are used to reconstruct gestation lengths and age at weaning in the extinct lemurs, only data for extant species were analyzed. Finally, since multiple comparisons can inflate Type I error, a Bonferroni correction was applied; however, the correction was applied to the arcades separately. Scripts of the R code are available in Appendix C.

Results

Objective 1: Molar Chronologies in *Avahi laniger* and *Indri indri*

One very small component of *Indri* dental development had previously been assessed. Catlett et al. (2010) reported prenatal M^1 crown formation for this specimen of *I. indri* to help inform a developmental model used to estimate a minimum gestation length for *M. globiceps*. The full maxillary molar chronology for this specimen is presented in this study (Figure 4.2 and Table 4.5). For the *I. indri*, it was only possible to estimate CFT for the M^1 and M^2, but not for the M^3 due to fractures in the cervical enamel. It was possible to calculate prenatal M^3 CFT, as the neonatal line was identified in all three teeth (Figure 4.2 and Table 4.5).

A molar chronology for *A. laniger* is presented in Figure 4.3 and Table 4.6. The

approximate age at death for *A. laniger* was known for this individual (~2.5 months), which was used to validate the CFTs. The neonatal line was identified in all three molars and CFTs were estimated for all three molars (i.e., M^1, M^2, M_3) as well.

Objective 2: Indriid-Palaeopropithecid Dental Developmental Data Comparisons

Figure 4.4 shows a comparison of the available M1 and M2 CFT data within the indriid-palaeopropithecid clade. Almost all of the M1 and M2 crowns develop *in utero* for *A. laniger*, and in *I. indri*, 36.6% and 32.5% of the M1 and M2, respectively, develop *in utero*. As expected, *A. laniger* and *I. indri* exhibit extremely fast molar development, which is characteristic for this clade. Surprisingly, the two species with the greatest proportion of M1 prenatal enamel were *A. laniger*, the smallest species in the indriid- palaeopropithecid clade, and *P. ingens*, the largest representative in this clade for which dental developmental data are available.

Results for associations among body size, brain size, and dental developmental data in the indriids and palaeopropithecids are presented in Table 4.7. Based on previous research, it was expected that brain size, as opposed to body size, would be more highly correlated with various aspects of molar crown development. This expectation was not met, as neither brain size nor body size significantly correlated with any aspect of total, prenatal, or postnatal CFTs (Table 4.7).

Objective 3: Lemurs and the Inhibitory Cascade Model

The expectation was that the lemurs would adhere to the IC model; however, there were mixed results. Figure 4.5 presents the results from the RMA for both the maxillary and mandibular molars. Both the maxillary and mandibular molars adhered to the predictions of the IC model (i.e., slope = 2.0, y-intercept = -1.0), as outlined by Kavanagh et al. (2007). For the maxillary molars (Fig 4.5a), R^2=0.72 ($p<0.001$), slope=1.92 (p=0.74, not significantly different from 2.0), and y-intercept = -1.29 (p=0.22, not significantly different from -1.0). For the mandibular molars (Fig. 4.5b), R^2=0.72 ($p<0.001$), slope=2.66 (p=0.058, not significantly different from 2.0), y-intercept=-1.77 (p=0.067, not significantly different from -1.0). As illustrated from the scatterplots (Fig. 4.5a-b), *Megaladapis edwardsi* appears to be an influential outlier. When *M. edwardsi* is removed, R^2 values are no longer significant (i.e., for maxillary molars R^2 = 0.18 (p=0.052) and mandibular molars R^2 =0.17 (p=0.13)).

Molar size ratios from lemur taxa were also compared within a morphospace based on Polly (2007). Figures 4.6 and 4.7 illustrate how the maxillary and mandibular molars, respectively, disperse within a morphospace. For the maxillary molars, several of the species fall within the purple space (representing the non-permissible morphospace), which is the area where the molar size pattern is M1 < M2 > M3, indicating that these species do not adhere to the linear predictions of the IC model. As illustrated in Figure 4.7, approximately four species did not follow the predictions of the IC model for the mandibular molars.

As discussed, another expectation of the IC model is that the middle tooth position, in this case the M2, will comprise 33% of the total molar area of the molar row.

Figures 4.8 and 4.9 are boxplots showing the distribution of the percentage of area that the M2 comprises in both the maxillary and mandibular molar rows. Although statistical tests were not conducted to assess if they were significantly different from 33%, trends can be observed. *D. madagascariensis* particularly stands out, as both the maxillary and mandibular M2s comprise ~40-41% of the total molar area. Interestingly, most of the M^2s from the lemurs comprise more than 33% of the total molar area (Figure 4.8), and *H. griseus* is the only exception, with the M_2 comprising ~33% of the total maxillary molar area. Palaeopropithecidae exhibit a broad range of variation in the amount of area the M^2 occupies in the maxillary molar row, with all the values exceeding 33% and even overlapping with *D. madagascariensis* (Figure 4.8). In contrast to the M^2, the M_2 comprises ~33% of the total mandibular molar area in several lemur taxa, but not all (Figure 4.9). Still the percentage the M_2 occupies in comparison to the M^2 is much less and, aside from the aye-aye, the M_2 does not exceed >37% of the mandibular molar area.

Figures 10a-h and Figures 4.11a-h assess the linear relationships (i.e., OLS regressions) among the molar triplets for each species, similar to an approach used by Evans et al. (2016), without the specific criteria of the slope to be 2.0 and the y-intercept to be -1.0. Most of the linear relationships among the molar triplets for lemurs were not significant; however, given the small sample sizes for each species, the lack of significance is, perhaps, not surprising. For example, some species have only one individual and the predictions of the IC model do not necessarily hold for intra-individual variation, as seen in the molars of some great apes and humans (Daly et al., 2015); therefore, it is best to work with species means (Evans et al., 2016). In other cases, the species may truly not exhibit a linear pattern for the M1-M2-M3. Therefore,

particularly with the limited sample sizes, the linear plots enable a visual comparison of the molar size pattern within the M1-M2-M3 triplet.

None of the maxillary molar triplets were significant at the α-level = 0.05 (Figures 4.10a-h). Some of the linear relationships were significant in the mandibular molar row. *C. medius* (Figure 4.11b) exhibited a significant linear relationship as did *P. verreauxi* (Figure 4.11d). Although not significant, *M. edwardsi* displayed an opposite trend compared to the other lemur taxa; the maxillary and mandibular molar rows exhibited a linear trend where the largest tooth was the M3 (Figures 4.10g and Figures 4.11g).

Objective 4: Correlations among Molar Size and Life History Variables

Correlation results for both Pearson's correlation coefficients and Spearman's rho are presented in Table 4.8. Correlation results are presented for comparisons among log body size, log brain size, log age at weaning, and log gestation length to test whether the data set yielded significant correlations. As expected, brain size, body size, and the life history variables were significantly correlated among each other (Table 4.8, the non-shaded area of the table). Since multiple comparisons were being conducted, a Bonferroni correction was applied separately for the comparisons among the maxillary and mandibular molars (the differently shaded areas of grey in Table 4.8). The results in red indicate discrepancies between the two statistical methods. The expectation was that molar size should be significantly correlated with all the variables, especially since body and brain size, gestation length, and age at weaning are all interrelated.

Based on the Pearson's correlation coefficient, all molar areas were significantly

correlated with body size. There was a discrepancy between the Pearson's correlation coefficient and Spearman's rho result for the M^3. Based on Pearson's correlation coefficient, all the molar areas were significantly correlated with brain size, with the exception of the M^3; however, there were several more discrepancies between the two statistical methods in the comparisons with brain size. Interestingly, not one of the maxillary molar areas was significantly correlated with age at weaning. Based on Pearson's correlation coefficient, all of the mandibular molar areas were significantly correlated with age at weaning; however, all of these comparisons yielded discrepancies between the two statistical methods. One final note, the values bolded in Table 4.8 are the highest significant Pearson's correlation coefficients. Interestingly, M_2 molar area appears to have strongest correlations with body and brain size, as well as, age at weaning compared to all other molar positions.

Discussion

The molar CFTs for *A. laniger* and *I. indri* support previous research that found indriids to develop their molars extremely fast, regardless of body size (e.g., Godfrey et al., 2005). For example, *P. ingens* is the largest bodied palaeopropithecid for which there are histological data (Schwartz et al., 2002). Interestingly, *A. laniger*, the smallest bodied indriid and smallest member of the indriid-palaeopropithecid clade as whole, develops similar proportions of M1 enamel *in utero* (i.e., 84.6% in *P.ingens* and 96.6% *A. laniger*). The finding that *A. laniger* and *P. ingens* share similar proportions of prenatal M1 development but are vastly different in body size may suggest that the greater

proportion of M1 development *in utero* is possibly due to convergent evolution.

Schwartz et al. (2002) and Godfrey et al. (2006) were able to develop a method to estimate gestation lengths for extinct lemur species by using three traits found in lemur dental development and reproductive ecology. First, nearly all lemur species, except aye- ayes and bamboo lemurs, are seasonal breeders (e.g., Fleagle, 2013; Sterling, 1994) that participate in a synchronous weaning cycle (Wright, 1999; Wright et al., 2005). Second, the M1 does not initiate until after the first trimester (Schwartz et al., 2002; Schwartz et al., 2005). Third, closely related taxa share gestation lengths (Martin, 1990; Kamilar and Cooper, 2013). For example, *P. verreauxi* has, on average, a gestation length of ~157 days. Using one individual to represent the species mean, the number of days required to form the prenatal M1 crown is 94 days. Therefore, dividing M1 prenatal enamel formation time by the gestation length yields an index of ~0.60 (i.e., 94 days/157 days=0.60). Catlett et al. (2010) confirmed that *I. indri* also had an index of ~0.59-0.60, and then applied the approach to *M. globiceps* to estimate the gestation length of this extinct lemur to be ~207 days (Catlett et al., 2010, see Figure 5). Given that both *I. indri* and *P. verreauxi* yielded a 'gestation-M1 prenatal' index of ~0.60, it is expected that *A. laniger* should also have an index of ~0.60; however, this is not the case.

The gestation model as outlined in the Godfrey et al. (2006) and Catlett et al. (2010) suggests that for *A. laniger* the gestation length is 193 days (114/0.59 = 193 days), which is much longer than the currently estimated gestation length (i.e., ~153 days) from behavioral observations in wild populations. While this model works for *P. verreauxi* and *I. indri*, it is noteworthy that they have similar proportions of prenatal M1

development (49.2% and 36.6% respectively; see Figure 4.4) compared to *A. laniger*, which has nearly 97% of the crown developed *in utero*. Given that *M. globiceps* had approximately 46.4% of the prenatal M1 crown developed (very similar to *P. verreauxi)*, the 0.59-0.60 index still seems appropriate to apply to this species, which estimates the *M. globiceps* gestation length to be ~6.9 months (Catlett et al., 2010). Perhaps, in this instance, *A. laniger* is a more suitable model for *P. ingens*, as they share the trait of having a large proportion of the M1 crown develop prenatally (i.e., 84.6% of the M1 crown is formed at birth). An index based on *A. laniger* is ~0.75 (i.e., 114 days) for prenatal M1 CFT/gestation length 153 days = 0.75). Applying this ratio to *P. ingens* yields an estimated gestation length of ~249 days (187/0.75 = 249 days) or ~8.3 months, a value that aligns more closely with the original gestation length estimated by Schwartz et al. (2002) (i.e., 6-9 months) than the estimate suggested by Godfrey et al. (2006) (i.e., 10.5 months). Additional consideration of the phylogenetic relationships for the proportion of M1 development *in utero*, a variable used to estimate gestation length in this clade, may be providing interesting insights into the relationship between dental development and gestation length in lemurs.

The genera *Avahi* and *Propithecus* each comprise approximately nine species (Mittermeier et al., 2008; Fleagle, 2013). Future histological analyses may be able to test the extent of interspecific variation present in the percentage of M1 prenatal crown development. Technological advances, such as the high-resolution images generated by the synchrotron (e.g., Smith et al., 2007), now permit imaging of the internal microstructures of teeth noninvasively, a useful methodology to protect rare fossils.

Perhaps a combination of these two methodologies would enable the estimation of gestation lengths for the remaining species of the palaeopropithecid clade (e.g., *P. maximus* compared to *P. ingens*), including the largest lemur known to have lived, *Archaeoindris fontoynontii*, if an infant jawbone of this species is ever recovered from the fossil record.

The hypothesis that the smallest-bodied indriid, *Avahi*, might be a better extant model to estimate the gestation length of the large-bodied, *Palaeopropithecus*, is just one example of how body size is possibly a relatively unreliable predictor for dental development and other life history variables in this clade. The lack of significant correlations between various aspects of M1 and M2 CFTs and body and brain size lends greater support to the hypothesis that these traditional measures of size are unreliable predictors within the indriid-palaeopropithecid clade. This is in contrast to many haplorhines and some other Malagasy lemurs. In many haplorhines, Macho (2001) reported significant correlations among M1 CFTs, brain size, and female body mass. When both the extant and extinct lemurs are included, the significant relationship between M1 CFTs and brain size holds, but not between M1 CFT and female body mass (Schwartz et al., 2005). As suggested by previous work, it is highly likely that ecological and life history variables, such as dental precocity at weaning, are better predictors of the rapid dental development that characterizes the indriid-palaeopropithecid clade (e.g., Godfrey et al., 2002; Godfrey et al. 2003).

Although CFTs are not associated with body size in lemurs, the maximum molar areas are significantly associated with body and brain size in extant lemurs. In the analyses presented in this study (Table 4.8), brain and body size significantly correlated

with several maxillary and mandibular molar positions, with the M_2 having the highest Pearson's correlation coefficients (i.e., body size: r=0.90, p-value ≤ 0.001 and brain size: r=0.87, p-value ≤ 0.001).

Palaeoanthropologists have demonstrated several scaling relationships comparing molar size with other measures of size, such as body and face size (e.g., Gingerich et al., 1982; Scott, 2012). Therefore, perhaps is not surprising that molar size correlates with body and brain size in extant lemurs. Evidence also exists that molar size may influence fitness. Degusta et al. (2003) report that selection may be targeting molar breadth in a population of howler monkeys (*e.g., Alouatta*), as monkeys with smaller molars do not survive weaning. Given that dental precocity is a target of selection in many lemurs (e.g. Godfrey et al. 2003), perhaps future research may find a similar pattern among lemurs, where weanlings with larger molars are more likely to survive. There is some evidence in this study (i.e., Chapter 4) that molar size may be associated with the timing of weaning. Interestingly, molar size did not consistently correlate with gestation length, but mandibular molar size did correlate with age at weaning, at least when the Pearson's correlation coefficients are considered (Table 4.8). Again, although all the mandibular molars consistently correlated with age at weaning, the M_2 maximum area exhibited the highest correlation with age at weaning in extant lemurs (i.e., r=83.6, p-value ≤ 0.001). All indriids minimally have M1 and M2 present at weaning. Given that vestigial deciduous teeth characterize the indriid-palaeopropithecid clade and are shed very early, the presence of M_2 may be critical for weanlings and so the timing of M_2 emergence may be strongly linked to weaning. Further exploration on associations

between M_2 and weaning may be warranted for other lemurs and non-Malagasy primates, as the emergence of M_2 seems to coincide with weaning in some great ape species (Chapter 3). The reoccurrence of M_2 area as having the strongest associations with the variables considered in this study is of interest when placed within the context of the IC model. As discussed, on average, there is a linear relationship among the primary postcanine dentition, and within the molar row, there is only one tooth position with the maximum tooth size, which is hypothesized to be the location of a developmental 'reversal' in the ratio of activators and inhibitors (e.g., Evans et al., 2016). If life history and ecological variables influence the selection of larger teeth (or a particular tooth when contextualized within the development of the masticatory apparatus), then, perhaps, the presence of a possible developmental reversal along the primary postcanine tooth row may be related to these external environmental and functional factors. Variation in such factors might select for a particular balance of inhibitor/activator ratios; thus, the expectation would be that the tooth positions most highly correlated with diet, life history, and other ecological variables would also be the location of the reversal.

The specific linear relationship (i.e., slope = 2.0, y-intercept = -1.0) barely held in both the mandibular and maxillary molars. For the maxillary molars, it appears the linear relationship between the M2/M1 and M3/M1 ratios shifted (Figure 5a). Exploration of whether this is a signal for a developmental offset between the maxillary and mandibular molars in lemurs requires further investigation. Another possible explanation is that the offset may be related to the size of the M^2. While M^1 and M^2s seem to be nearly equal in

size for many of the species examined, the M^2 comprises a much larger proportion of the molar row than expected.

Except for *H. griseus*, the proportion of M^2 that occupies the maxillary molar triplet was greater than the predicted 33% in all species examined; however, for many of the taxa, the M_2s occupy ~33% of the molar triplet area, as predicted. The aye-aye is an interesting exception, as both M2s comprise a much larger proportion of the molar row (i.e., ~41%) and fall outside the predicted regions of the morphospace (white space in Figures 4.6 and 4.7) associated with the IC model. In addition, Palaeopropithecidae have M2s larger than the expected 33%; however, unlike the molars of *D. madagascarensis*, the maxillary and mandibular molar rows in the palaeopropithecids fell within the predicted region of the morphospace associated with the IC model. The indriids also fell within the predicted morphospace, with the exception of the mandibular molars from *A. laniger*; however, this species fell very close to the predicted line, as all the molars are very similar in size. While, perhaps, the smaller than expected M_2 in *A. laniger* may be an artifact of sample size, Godfrey et al. (2005) also reported that M_2s are slightly smaller than the M_1 and M_3. The lemurids also have larger maxillary and mandibular M2s than the expected 33%, and *L. catta*, like *D. madagascariensis*, did not fall within the predicted morphospace for the IC model. Among lemurids, *L. catta* in particular displays a trend where the M2 is the largest tooth both in the maxillary and mandibular molar rows. Unlike the indriids and *Daubentonia*, where some of the deciduous premolars have been completely lost and some diminished in size, *L. catta* still possesses three deciduous premolars (Swindler, 2002). In general, when molar triplets fall outside

the permissible region of the morphospace (i.e., $M_1 < M_2 > M_3$), it is quite possible that if the deciduous dentition were included in the analysis the pattern would be one where there is a linear increase in the primary postcanine row until the M_2. At the M_2, there might be a developmental reversal where inhibitors increase (or activators decrease), resulting in the early arrest of M_3 development. For example, perhaps, the primary postcanine size gradient in the *L. catta* is dp3<dp4<M1<M2>M3. Future work that includes the deciduous premolars will help resolve whether the overall size gradient in the ring-tailed lemurs (and other lemur specie) adhere to the IC model. In a situation where the pattern is $M_1 > M_2 < M_3$, as seen here for *A. laniger*, or like Polly (2007) observed with horses, there is no clear explanation. Perhaps, as the histological analysis revealed, the extremely early initiation of the M_1 and nearly coincident initiation of the M_2 affect the developmental cascade in a manner not yet understood.

Godfrey et al. (2003) documented that dental precocity and dp4/M1 size ratio is a good predictor for age at weaning, and small dp4s relative to the M1 are found in species that wean early. The IC model predicts that the anteriormost postcanine tooth affects the subsequent development of the posterior teeth that a developmental cascade. Many of the lemur species analyzed in this study adhered to aspects of the IC model, particularly the mandibular molars, but a tremendous amount of variation still needs further explanation. In order to conduct a more robust assessment of the developmental cascade pattern along the entire primary postcanine tooth row in lemurs, it is necessary to include the deciduous dentition.

Conclusion

Evans et al. (480:2016) state: "Whereas selective pressures emphasizing function, such as changing bite force, have been used to explain the variation in tooth proportions, only by including development can one explain the details of the changes." In the case of many lemurs, Godfrey et al. (2002; Godfrey et al. 2003) hypothesized that the target of selection is dental precocity at weaning and that dp4/M1 size ratios regressed against dental precocity is a good predictor for age at weaning. The hyper-acceleration of dental development in the indriid-palaeopropithecid clade is likely a combination of selection targeting dental precocity at weaning by sacrificing the deciduous dentition to accelerate the development and emergence of the molars, resulting in large proportions of molar development *in utero*. While previous work has focused primarily on the M_1 and its relationship to life history variables, the developmental and functional role of the M_2 may be worth detailed examination as well. Molar size directly reflects the developmental cascade and timing of initiation, and the rapid dental development observed in the indriid-palaeopropithecid clade may also include selection acting not only acting on the timing of M_2 emergence, but also on the size of the M_2 (i.e., a possible phenotype of interest).

References

Ali, JR., Huber, M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. Nature 463:653-656.

Ankel-Simons, F. 2007. An Introduction to Primate Anatomy. (3 ed.). San Diego: Academic Press.

Antoine, D., Hillson, S. Dean, MC. 2009. The developmental clock of dental enamel: A test for the periodicity of prism cross-striations in modern humans and an evaluation of the most likely sources of error in histological studies of this kind. J Anat 214:45-55.

Asahara, M. 2013. Unique inhibitory cascade pattern of molars in canids contributing their potential to evolutionary plasticity of diet. Evol Evol 3:278-285.

Barrickman, NL., Lin, MJ. 2010. Encephalization, expensive tissues, and energetics: An examination of the relative costs of brain size in strepsirrhines. Am J Phys Anthrpol 143:579-590.

Bernal, V., And Gonzalez, PN. And Perez, S. I. 2013. Developmental processes, evolvability, and dental diversification of New World Monkeys. Evol Biol 40:532-541.

Bromage, TG. 1991. Enamel incremental periodicity in the pig-tailed macaque: A polychrome fluorescent labeling study of dental hard tissues. Am J Phys Anthropol 86:205-214.

Bromage, TG., Lacruz, RS., Hogg, R., Goldman, HM., Mcfarlin, SC., Warshaw, J., Dirks, W., Perez-Ochoa, A., Smolyar, I., Enlow, DH., Boyd, A. 2009. Lamellar bone is an incremental tissue reconciling enamel rhythms, body size, an organismal life history. Calcif Tissue Int 84:388-404.

Burney, DA., Burney, LP., Godfrey, LR., Jungers, WL., Goodman, SM., Wright, HT., Jull, AJT. 2004. A chronology for late prehistoric Madagascar. J Hum Evol 47:25-63.

Burns, SJ., Godfrey, LR., Faina, P., Mcgee, D., Hardt, B., Ranivoharimanana, L., Randrianasy, J. 2016. Rapid human-induced landscape transformation in Madagascar at the end of the first millennium of the common era. Quaternary Science Reviews 134:92-99.

Catlett, KK., Schwartz, GT., Godfrey, LR. Jungers, WL. 2010. “Life history space”: A multivariate analysis of life history variation in extant and extinct malagasy lemurs. Am J Phys Anthropol 142:391-404.

Charnov, EL., Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. Evol Anth 1:191-194.

Copes, LE., Schwartz, GT. 2010. The scale of it all: Postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law. Paleobiology 36:188-203.

Crowley, BE. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quatern Sci Rev 29:2591-2603.

Daly, ES and Catlett, KK. 2014. A test of inhibitory cascade (IC) model on primate deciduous premolars. Am J Phys Anthropol Suppl 58:102.

Daly, ES, Catlett, KK, Paul, KS, Nesse, HP. 2015.An intraspecific analysis of the inhibitory cascade (IC) model in gorillas, chimpanzees, and modern humans. Am J Phys Anthropol Suppl. 60:115.

Dean, MC. 1995. The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 (*Homo habilis*). In: Moggi-Cecchi, J., editor. Aspects of Dental Biology: Paleontology, Anthropology, and Evolution. Florence: International Institute for the Study of Man. pp 239–265.

Dean, MC. 1993. Daily rates of dentine formation in macaque tooth roots. Int J Osteoarchaeol 3:199-206.

Dean, MC., Beynon, AD., Reid, DJ. Whittaker, DK. 1993. A longitudinal study of tooth growth in a single individual based on long-and short-period incremental markings in dentine and enamel. Int J Osteoarchaeol 3:249-264.

Dewar, RE., Richard, AF. 2007. Evolution in the hypervariable environment of Madagascar. Proc Natl Acad, USA 104:13723-13727.

Dirks, W. 2003. Effect of diet on dental development in four species of catarrhine primates. Am J Primatol 61:29-40.

Douglass, K., Zinke, J. 2015. Forging ahead by land and by sea: archaeology and paleoclimate reconstruction in Madagascar. Afr Archaeol Rev 32:267-299.

Eaglen, RH. 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. Am J Phys Anthropol 66:307-315.

Evans, AR, Daly, ES, Catlett, KK, Paul, KS, King, SJ, Skinner, MM, Nesse, HP, Hublin, JJ, Townsend, GC, Schwartz, GT, Jernvall, J. 2016. A simple rule governs the evolution and development of hominin tooth size. Nature 530: 477-480.

Fitzgerald, C., Saunders, S., Bondioli, L. Macchiarelli, R. 2006. Health of infants in an imperial roman skeletal sample: Perspective from dental microstructure. Am J Phys Anthropol 130:179-189.

Fleagle, JG. 2013. Primate Adaptations and Evolution. London: Academic Press.
Ganzhorn, JU. 1995. Cyclones over Madagascar: fate or fortune. Ambio 24:125-124.

Gingerich, PD., Smith, BH. Rosenberg, K. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. Am J Phys Anthropol 58:81-100.

Godfrey, LR., Jungers, WL. 2003. The extinct sloth lemurs of Madagascar. Evol Anthropol 12:252-263.

Godfrey, LR., Rasoazanabary, E. 2012. Demise of the bet hedgers: A case study of human impacts on past and present lemurs of Madagascar. In: Sodikoff, G. M., editor. The Anthropology of Extinction: Essays on Culture and Species Death. pp 165–199

Godfrey, LR., Crowley, BE., Muldoon, KM., Kelley, EA., King, SJ., Best, AW. Berthaume, MA. 2015. What did *Hadropithecus* eat, and why should paleoanthropologists care. Am J Primatol 9999:1-15.

Godfrey, LR., Crowley, BE. Dumont, ER. 2011. Thinking outside the box: A lemur's take on hominin craniodental evolution. Proc Natl Acad Sci USA 108:E742.

Godfrey, LR., Jungers, WL., Reed, KE., Simons, EL. Chatrath, P. 1997. Primate subfossils: inferences about past and present primate community structure. In: Goodman, S., Patternson, B., editors. Natural and Human Influenced Environmental Change in Madagascar. pp 218–256

Godfrey, LR., Jungers, WL., Schwartz, GT. Irwin, MT. 2008. Ghosts and Orphans: Madagascar's Vanishing Ecosystems. Elwyn Simons: A Search for Origins. Chicagot: University of Chicago. pp 361–395

Godfrey, L., Petto, AJ. Sutherland, MR. 2002. Dental ontogeny and life-history strategies: The case of the giant extinct Indroids of Madagascar. In: Plavcan, JM., Kay, RF., Jungers, WL., van Schaik, CP. Reconstructing Behavior in the Primate Fossil Record. New York: Kluwer Academic/Plenum. pp 113–157.

Godfrey, LR., Samonds, KE., Jungers, WL. Sutherland, MR. 2001. Teeth, brains, and primate life histories. Am J Phys Anthropol 114:192-214.

Godfrey, LR., Samonds, KE., Jungers, WL., Sutherland, MR. Irwin, MT. 2004. Ontogenetic correlates of diet in Malagasy lemurs. Am J Phys Anthropol 123:250-276.

Goodman, AH., Rose, JC. 1990. Assessment of systemic physiological perturbations from dental enamel hypoplasias and associated histological structures. Am J Phys Anthropol 33:59-110.

Guatelli-Steinberg, D., Benderlioglu, Z. 2006. Brief communication: Linear enamel hypoplasia and the shift from irregular to regular provisioning in Cayo Santiago rhesus monkeys (*Macaca mulatta*). Am J Phys Anthropol 131:416-419.

Halliday, TJD., Goswami, A. 2013. Testing the inhibitory cascade model in Mesozoic and Cenozoic mammaliaforms. BMC Evol Biol 13:1-11.

Hawkes, K., O'Connell, JF., Jones, NGB., Alvarez, H. Charnov, EL.1998. Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336-1339.

Hogg, RT., Walker, RS. 2011. Life-history correlates of enamel microstructure in cebidae (Platyrrhini, Primates). Anat Rec 294:2193-2206.

Hogg, RT., Godfrey, LR., Schwartz, GT., Dirks, W. Bromage, TG. 2015. Lemur biorhythms and life history evolution. PLOS ONE 10:e0134210.

Hrdy, SB. 2009. Mothers and Others: The Evolutionary Origins of Mutual Understanding. Harvard University Press: Belknap Press.

Irwin, MT. 2007. Ecologically Enigmatic Lemurs: The sifakas of the Eastern forests (*Propithecus candidus, P. diadema, P. edwardsi, P. perrieri*, and *P. tattersalli*). In: Gould, L., Sauther, ML., editors. Lemurs: Ecology and Adaptation. pp 305–326

Isler, K., van Schaik, CP. 2009. The expensive brain: A framework for explaining evolutionary changes in brain size. J Hum Evol 57:392-400.

Isler, K., van Schaik, CP. 2012. How our ancestors broke through the gray ceiling: Comparative evidence for cooperative breeding in early *Homo*. Curr Anthropol 53:S453- S465.

Janson, CH., van Schaik, CP. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira, ME., Fairbanks, LA., editors. Juvenile Primates: Life history, development, and behavior. Chicago: University of Chicago Press. pp 57–74.

Järvinen, E., Valimaki, K., Pummila, M., Thesleff, I. Jernvall, J. 2008. The taming of the shrew milk teeth. Evol Dev 10:477-486.

Jungers, WL., Demes, B. Godfrey, LR. 2008. How big were the "giant" extinct lemurs of Madagascar? In: Fleagle, JG., Gilbert, CC., editors. Elwyn Simons: A Search for Origins. Chicago, IL: University of Chicago. pp 343–360.

Kamilar, JM., Cooper, N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. Philos T R Soc B 368:1-10.

Kavanagh, KD., Evans, AR. Jernvall, J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449:427-432.

Kawasaki, K., Tanaka, S. Ishikawa, T.. On the incremental lines in human dentine as revealed by tetracycline labelling. J Anat 123:427-236.

Kelley, J., Schwartz, GT. 2010. Dental development and life history in living African and Asian apes. Proc Natl Acad Sci USA 107:1035-1040.

Kistler, L., Ratan, A., Godfrey, LR., Crowley, BE., Hughes, CE., Lei, R., Cui, Y., Wood, ML, Muldoon, KM, Andriamialison, H., McGraw, JJ, Tomsho, LP, Schuster, SC., Miller, W., Louis, EE, Yoder, AD, Malhi, RS., Perry, GH. 2015. Comparative and population mitogenomic analyses of Madagascar's extinct, giant subfossil lemurs. J Hum Evol
79:45-54.

Leigh, SR., Shea, BT. 1996. Ontogeny of body size variation in African apes. Am J PhysAnthropol 99:43-65.

Macho, GA. 2001. Primate molar crown formation times and life history evolution revisited. Am J Primatol 55:189-201.

Maclean, EL., Barrickman, NL., Johnson, E.M. Wall, CE. 2009. Sociality, ecology, and relative brain size in lemurs. J Hum Evol 56:471- 478.

Mahoney, P. 2011. Human deciduous mandibular molar incremental enamel development. Am J Phys Anthropol 144:204-214.

Martin, RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293:57-60.

Martin, RD.1990. Primate Origins and Evolution: A Phylogenetic Reconstruction. Chapman and Hall.

Mittermeier, RA., Ganzhorn, JU., Konstant, WR., Glander, K., Tattersall, I., Groves, CP., Rylands, AB, Hapke, A., Ratsimbazafy, J., Mayor, MI., Louis Jr., EE., Rumpler, Y., Schwitzer, C. Rasoloarison, RM. 2008. Lemur diversity in Madagascar. Int J Primatol 29:1607-1656.

Molnar, S., Przybeck, TR., Gantt, DG., Elizondo, RS. Wilkerson, JE. 1981. Dentin apposition rates as markers of primate growth. Am J Phys Anthropol 55:443-453.

Nanci, A. 2013. Ten Cate's Oral Histology: Development, Structure, and Function (8 ed.). St. Louis: Elsevier Mosby.

Navarrete, A., van Schaik, CP. Isler, K. 2011. Energetics and the evolution of human brain size. Nature 480:91-93.

Ohba, M., Samonds, KE., Lafleur, M., Ali, JR. Godfrey, LR. 2016. Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. Palaeogeogr Palaeocl 441:688-695.

Olofsson, H., Ripa, J. Jonzen, N. 2009. Bet-hedging as an evolutionary game: The trade- off between egg size and number. P R Soc B 276:2963-2969.

Orlando, L., Calvignac, S., Schnebelen, C., Douday, CJ., Godfrey, LR. Hänni, C. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evol Biol 8:1-9.Perez, VR., Godfrey, LR., Nowak-Kemp, M., Burney, DA., Ratsimbazafy, J.
Vasey, N. 2005. Evidence of early butchery of giant lemurs in Madagascar. J Hum Evol 49:722-742.

Polk, JD., Williams, SA., Peterson, JV., Roseman, C. Godfrey, LR. 2010. Subchondral bone apparent density and locomotor behavior in extant primates and subossil lemurs *Hadropithecus* and *Pachylemur.* Int J Primatol 31:275-299.

Polly, PD. 2007. Evolutionary biology: Development with a bite. Nature 449:413-415.

Pontzer, H., Raichlen, DA., Gordon, AD., Schroepfer-Walker, KK., Hare, B.O, Äôneill, MC., Muldoon, KM, Dunsworth, H., Wood, BM., Isler, K.,Burkart, J., Irwin, M., Shumaker, RW, Lonsdor, EV, Ross, SR. 2014. Primate energy expenditure and life history. Proc Natl Acad Sci USA111:1433-1437.

Poux, C., Madsen, O., Marquard, E., Vieites, DR., De Jong, WW. Vences, M. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Systematic Biology 54:730-719.

Renvoisé, E., Evans, A. R., Jebrane, A., Labruère, C., Laffont, R. Montuire, S. 2009. Evolution of mammal tooth patterns: New insights from a developmental prediction model. Evolution 63:1340-1327.

Reid, DJ., Schwartz, GT., Dean, C. Chandrasekera, MS. 1998. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J Hum Evol 35:427-448.

Reid, DJ., Ferrell, RJ. 2006. The relationship between number of striae of Retzius and their periodicity in imbricational enamel formation. J Hum Evol 50:195-202.
Richard, AF., Dewar, RE., Schwartz, M. Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). J Zool 256:421-436.

Roff, DA. 2002. Life history evolution. Sunderland, Massachusetts: Sinauer Associates, Inc.

Rubenstein, DR. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proc Natl Acad, USA 108:10816-10822.

Rumpler, Y., Hauwy, M., Fausser, JL., Roos, C., Zaramody, A., Andriaholinirina, N, Zinner, D. 2011. Comparing chromosomal and mitochondrial phylogenies of the Indriidae (Primates, Lemuriformes). Chromosome Res 19:209-224.

Sacher, GA. 1959. Relation of lifespan to brain weight and body weight in mammals. London: Churchill.

Schroer, K., Wood, B. 2015. Modeling the dental development of fossil hominins through the inhibitory cascade. J Anat 226:150-162.

Schwartz, GT., Mahoney, P., Godfrey, LR., Cuozzo, FP., Jungers, WL. Randria, GFN. 2005. Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes):Implications for understanding life history variation in subfossil lemurs. J Hum Evol 49:702-721.

Schwartz, GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221-244.

Schwartz, GT., Samonds, KE., Godfrey, LR., Jungers, WL. Simons, EL. 2002. Dental microstructure and life history in subfossil Malagasy lemurs. Proc Natl Acad Sci, USA 99:6124-6129.

Schwartz, GT., Dean, MC. 2008. Charting the chronology of developing dentitions. In: Irish, JD., Nelson, GC., editors. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press. pp 219–233.

Schwitzer, C., Mittermeier, RA., Johnson, SE., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, Raxafindramanana, J., Louis Jr, EE, Chikhi, L., Colquhon, IC, Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T.,

Wright, PC. 2014. Averting lemur extinctions amid Madagascar's political crisis. Science 343:842-843.

Scott, JE. 2012. Molar size and diet in the strepsirrhini: Implications for size-adjustment in studies of primate dental adaptation. J Hum Evol 63:796-804.

Scott, JR., Godfrey, LR., Jungers, WL., Scott, RS., Simons, EL., Teaford, MF, Ungar, PS, Walker, A. 2009. Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. J Hum Evol 56:405-416.

Sibly, RM., Brown, JH. 2007. Effects of body size and lifestyle on evolution of mammal life histories. Proc Natl Acad Sci USA 104:17707-17712.
Smith, BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:134-142.

Smith, RJ. 2009. Use and misuse of the reduced major axis for line-fitting. Am J Phys Anthropol 140:476-486.

Smith, TM., Reid, DJ. Sirianni, JE. 2006. The accuracy of histological assessments of dental development and age at death. J Anat 208:125-138.

Smith, TM. 2006. Experimental determination of the periodicity of incremental features in the enamel. J Anat 208:125-138.

Smith, TM., Tafforeau, P., Reid, DJ., Grun, R., Eggins, S., Boutakiout, M. , Hublin, J-J. 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci USA 104:6128-6133.

Stearns, S.C. 1992. The evolution of life histories. New York: Oxford.

Sterling, EJ. 1994. Evidence for nonseasonal reproduction in wild aye-aye (*Daubentonia madagascariensis*). Folia Primatol (Basel) 62:46-53.

Swindler, DR. 2002. Primate dentition: an introduction to the teeth of non-human primates. (2nd ed.). Cambridge: Cambridge University Press.

Warton, DI., Duursma, RA., Falster, DS. Taskinen, S. 2012. Smatr 3 - An R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3:257-259.

Weisbecker, V., Goswami, A. 2010. Brain size, life history, and metabolism at the marsupial/placental dichotomy. Proc Natl Acad Sci, USA 107:16216-16221.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. New York: Springer.

Wilson, LB., Sánches-Villagra, MR., Madden, RH. Kay, RF. 2012. Testing a developmental model in the fossil record: Molar proportions in South American ungulates. Paleobiology 38:308-321.

Winchester, JM., Boyer, DM., St. Clair, EM., Gosselin-Ildari, AD., Cooke, SB. Ledogar, JA. 2014. Dental topography of platyrrhines and prosimians: Convergence and contrasts. Am J Phys Anthropol 153:29-44.

Wright, PC., Razafindratsita, VR., Pochron, ST. Jernvall, J. 2005. The Key to Madagascar Frugivores. In: Dew, JL., Boubli, JP., editors. Tropical Fruits and Frugivores: The Search for Strong Interactors. pp 121–138.

Table 4.1. Data compiled from the literature for extant lemur species.

Family	Species	Brain Size (g)	Body Mass (kg)	Gestation Length (days)	Age at Weaning (days)
Cheirogaleidae	*Cheirogaleus major*	6	0.4	65	47.14
Cheirogaleidae	*Cheirogaleus medius*	3	0.14	61	60.65
Cheirogaleidae	*Microcebus murinus*	2	0.065	61	40.45
Cheirogaleidae	*Microcebus rufus*	2	0.045	54.75	40
Cheirogaleidae	*Mirza coquereli*	6	0.312	89	136
Daubentoniidae	*Daubentonia madagascariensis*	46	2.555	167	197.7
Indriidae	*Avahi laniger*	10	1.207	153.3	149.65
Indriidae	*Indri indri*	36	6.335	153.3	244.55
Indriidae	*Propithecus diadema*	41	6.13	178.85	182.5
Indriidae	*Propithecus verreauxi*	27	2.955	157	182.5
Lemuridae	*Eulemur corotus*	21	1.18	126	NA
Lemuridae	*Eulemur fulvus*	27	2.292	124.1	182.5
Lemuridae	*Eulemur macaco*	25	2.39	124.1	135.05
Lemuridae	*Eulemur mongoz*	21	1.212	127.75	153.3
Lemuridae	*Eulemur rubriventer*	27	2.388	130	151.22
Lemuridae	*Hapalemur griseus*	15	0.709	138.7	120.45
Lemuridae	*Lemur catta*	24	2.21	135.05	178.85
Lemuridae	*Varecia variegata*	33	3.599	102.2	146
Lepilemuridae	*Lepilemur mustelinus*	10	0.777	135	76.21

The reported values are based on the means. Sources: Godfrey et al., 2004: MacLean et al., 2009; Kamilar and Cooper, 2013).

Table 4.2. Data compiled from the literature for extinct lemur species.

Family	Species	Brain Size (cm^3)	Body Mass (kg)	Gestation Length (days)	Age at Weaning (days)
Archaeolemuridae	*Archaeolemur majori*	93	18.2	175.2	610
Archaeolemuridae	*Hadropithecus stenogthus*	106	35.4	190	1095
Archaeolemuridae	*Archaeolemur edwardsi*	NA	26.5	NA	NA
Megaladapidae	*Megaladapis edwardsi*	136	85.1	248	380
Palaeopropithecidae	*Mesopropithecus globiceps*	40.5	11.3	212	201
Palaeopropithecidae	*Palaeopropithecus ingens*	80	41.5	249*	183
Palaeopropithecidae	*Archaeoindris fontoynonti*	NA	161.2	NA	NA
Palaeopropithecidae	*Babakotia radofilai*	NA	20.7	NA	NA
Palaeopropithecidae	*Palaeopropithecus maximus*	NA	45.8	NA	NA

* Schwartz et al., 2002 report an estimated gestation length of >187 days (6.23 months). Based on the available models, Godfrey et al. (2006) suggested was 321 days (~10.7 months) and this was the value used in Catlett et al. 2010. Using the new available data from *A. laniger*, the estimated gestation length for *P. ingens* is 249 days (see text for details), which is more closely aligned with the original gestation length estimated in Schwartz et al. (2002). Body and brain size estimates from Jungers et al. (2008) and Catlett et al. (2010).

Table 4.3 Molar areas (mm^2) for extant lemur species.

Family	Species	M^1	M^2	M^3	M_1	M_2	M_3
Cheirogaleidae	*C. major* (n=1)	11.8	12.5	9.8	8.2	7.7	7.6
Cheirogaleidae	*C. medius* (n=3)	6.7	7.1	4.4	4.8	4.7	4.6
Daubentoniidae	*D. madagascariensis* (n=1)	13.3	14.4	7.5	11.3	14.3	9.6
Indriidae	*A. laniger* (n=3)	17.9	16.4	10.8	13.2	11.8	12.9
Indriidae	*I. indri* (n=2-3)*	55.8	51.5	37	43.9	41.1	39
Indriidae	*P. verreauxi* (n=7)	39.3	40.7	20.9	31.2	30.2	29.1
Lemuridae	*E. fulvus* (n=4)	41.7	44.6	26.6	24.4	24.3	17.9
Lemuridae	*E. mongoz* (n=2)	40	41.4	20.3	25.4	24.1	15.9
Lemuridae	*E. rubriventer* (n=4)	41.9	37.6	22.4	26.6	24.8	16.5
Lemuridae	*H. griseus* (n=4)	23	23	23	15	16.1	12.9
Lemuridae	*L. catta* (n=2)	27.3	32.9	25	17	18.9	16.3
Lemuridae	*V. variegata* (n=5-8)*	56.9	56.8	29.7	39	32.9	20.4
Lepilemuridae	*L. mustelinus* (n=6)	11.9	11.9	8.7	8.6	8.4	8.4

When possible, values are based on the means. Sources: Swindler, 2002; Godfrey et al., 2006; Copes and Schwartz, 2010.

Table 4.4. Molar areas (mm^2) for extinct lemur species.

Family	Species	M^1	M^2	M^3	M_1	M_2	M_3
Archaeolemuridae	*Archaeolemur majori*	73.7	59.4	40	64.8	60.8	46.9
Archaeolemuridae	*Hadropithecus stenogthus*	136.7	118	65.4	NA	NA	NA
Archaeolemuridae	*Archaeolemur edwardsi*	92.2	75.4	52	NA	NA	NA
Megaladapidae	*Megaladapis edwardsi*	293	473.8	562	206.4	323.4	549.8
Palaeopropithecidae	*Mesopropithecus globiceps*	54.8	51.6	32.7	NA	NA	NA
Palaeopropithecidae	*Palaeopropithecus ingens*	245.2	239	80.1	185.4	161.5	121.8
Palaeopropithecidae	*Archaeoindris fontoynonti*	369.9	363.4	139.8	NA	NA	NA
Palaeopropithecidae	*Babakotia radofilai*	72.6	72.9	50	NA	NA	NA
Palaeopropithecidae	*Palaeopropithecus maximus*	234.3	227.1	89.2	NA	NA	NA

When possible, values are based on the means. Sources: Godfrey et al., 2006; Copes and Schwartz, 2010.

Table 4.5. Summary of dental developmental data for Indri indri. The periodicity was 2 in this individual.

Tooth Type	**M^1**	**M^2**	**M^3**
Cuspal Enamel Thickness (μm)	~445	~470	~530
Avg. Secretion Rate (μm/day)*	5.22	5.00	5.00
Total Cuspal Formation Time (days)	85	94	106
Number of Striae of Retzius	79	70	unk
Total Crown Formation Time (days)	**243**	**~234***	**unk***
Location of Neonatal Line	SR# 2	~380 μm**	~55 μm**
Time to form Prenatal Enamel (days)	89	76	11 days
Percentage of Enamel formed *In utero*	36.6% (89/243)	32.5% (76/234)	unk

* Due to fractures in the cervical region, it was difficult to obtain complete crown formation times. The crown formation time for the M^2 is the best estimate, and an estimate was not possible for the M^3.
** Relative to the enamel-dentine junction (EDJ) at the dentine horn.

Table 4.6. Summary of dental development data for Avahi laniger. The periodicity was 2 in this individual.

Tooth Type	**M_1**	**M_2**	**M^3**
Max. Cuspal Enamel Thickness (µm)	~350 µm	405µm	345µm
Avg. Secretion Rate (µm/day)*	~6.7µm	~6.1µm	~6.2µm
Total Cuspal Formation Time (days)	52 days	~60 days	56 days
Number of Striae of Retzius	33	30	31
Total Crown Formation Time (days)	**118**	**120**	**~115-118***
Location of Neonatal Line	#SR31	#SR25	~181 µm**
Time to form Prenatal Enamel (days)	114 days	110	94 days
Percentage of Enamel formed *In utero*	96.6%	91.7%	~82%

* Due to fractures in the cervical region, it was difficult to obtain complete crown formation times. The crown formation time for the M^3 is the best estimate.
** Relative to the enamel-dentine junction (EDJ) at the dentine horn.

TABLE 4.7. Correlation results for brain size, body size, and crown formation times (CFTs) in the indriid-palaeopropithecid clade. (n=5 for comparisons). The first value is Pearson's r and the second value is Spearman's rho.

Trait	Log Body Size	Log Brain Size
Log Brain Size	0.965 (p = 0.008)** 1.00 (p≤0.01) **	--
Log M1 CFT	0.610 (p = 0.275) 0.359 (p=0.553)	0.772 (p = 0.126) 0.359 (p= 0.553)
Log M1 Prenatal CFT	0.708 (p = 0.181) 0.600 (p = 0.285)	0.534 (p = 0.354) 0.600 (p= 0.285)
Log M1 Postnatal CFT	0.380 (p=0.528) 0.100 (p=0.873)	0.582 (p=0.304) 0.100 (p=0.873)
Log M2 CFT	0.741 (p=0.152) 0.872 (p=0.054)	0.869 (p=0.056) 0.872 (p=0.054)
Log M2 Prenatal CFT	0.314 (p=0.606) 0.400 (p=0.505)	0.058 (p=0.927) 0.400 (p=0.505)
Log M2 Postnatal CFT	0.639 (p=0.246) 0.100 (p=0.873)	0.808 (p=0.098) 0.100 (p=0.873)
Log M3 Prenatal CFT*	-0.294 (p=0.631) -0.200 (p=0.747)	-0.500 (p=0.391) -0.200 (p=0.747)

*Complete M3 CFT was not available (see text for details).

TABLE 4.8. Summary of correlations among molar size, body and brain size, and life history variables in extant lemurs.

Trait	Log Body Size	Log Brain Size	Log Gestation Length	Log Age at Weaning
Log Brain Size	0.970* 0.958* n=19	--	--	--
Log Gestation Length	0.872* 0.693* n=19	0.874* 0.702* n=19	--	--
Log Age at Weaning	0.897* 0.832* n=19	0.903* 0.870* n=18	0.878* 0.776* n=18	--
Log M^1 Maximum Area	0.828* 0.797* n=13	0.769* 0.714(p=0.006) n=13	0.476 0.085 n=13	0.737 0.550 n=13
Log M^2 Maximum Area	0.826* 0.775* n=13	0.783* 0.689* n=13	0.463 0.074 n=13	0.742 0.583 n=13
Log M^3 Maximum Area	0.757* 0.615 (p=0.025) n=13	0.699 0.548 n=13	0.448 0.061 n=13	0.664 0.440 n=13
Log M_1 Maximum Area	0.875* 0.846* n=13	0.805* 0.719(p=0.006) n=13	0.528 0.248 n=13	0.774* 0.613 (p=0.026) n=13
Log M_2 Maximum Area	**0.903*** **0.885*** **n=13**	**0.873*** **0.788*** **n=13**	0.598 0.256 n=13	**0.836*** **0.660 (p=0.014)** **n=13**
Log M_3 Maximum Area	0.885* 0.858* n=13	0.769** 0.727(p=0.005) n=13	0.618 0.302 n=13	0.805* 0.689(p=0.009) n=13

* $p \leq 0.004$. A Bonferroni correction was applied to each arcade (0.05/12=0.004) separately signified by the different shades of grey. The first value reported is the Pearson correlation coefficient, and the second value is Spearman's rho. Values in red indicate discrepancies between the two methods. Bolded values are the highest Pearson correlation coefficients (see text for details).

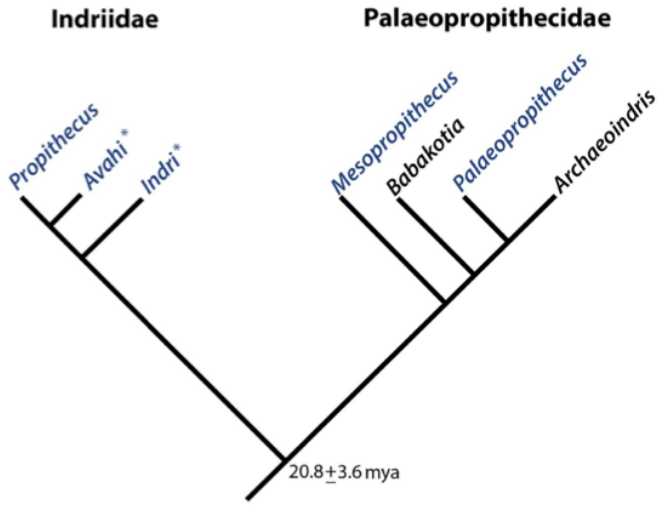


Figure 4.1. Phylogeny for the indriid-palaeopropithecid clade. Taxa included in this study are in blue. New dental developmental data based on histological techniques for taxa with an asterisk are presented in this study (*). Kistler et al. 2015 resolved the phylogeny for the indriids. *Indri* and *Avahi* shared a last common ancestor (LCA) ~18 mya. *Avahi* and *Propithecus* shared a LCA~14-13 mya. Sources: Godfrey and Jungers, 2003; Orlando et al., 2008; Kistler et al., 2015.

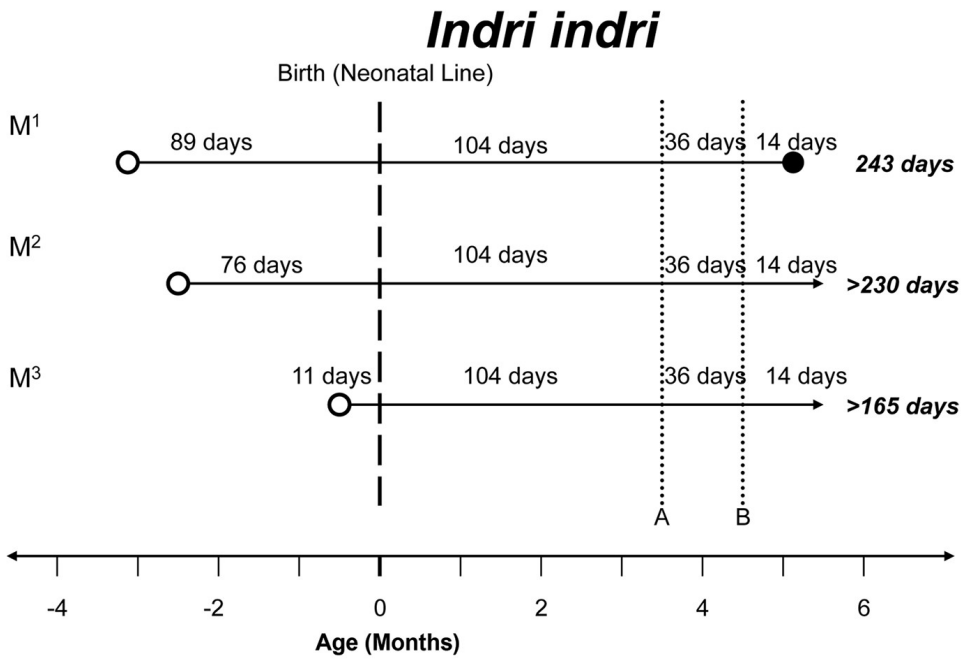


Figure 4.2. Molar chronology for Indri indri. The neonatal line and two accentuated lines were identified in the molar series. The M^1 initiates 89 days before birth and completes crown development 154 days after birth, which results in a total M^1 crown formation time of 243 days. The M^2 initiates 76 prior to birth and requires at least an additional 154 days to complete crown development. Since there were some fractures in the cervical enamel, it was difficult to obtain an estimated time for crown completion and 230 days is the best estimate possible for this specimen. A total crown formation was not possible to estimate for the M^3, but the M^3 also initiates *in utero* approximately 11 days prior to birth.

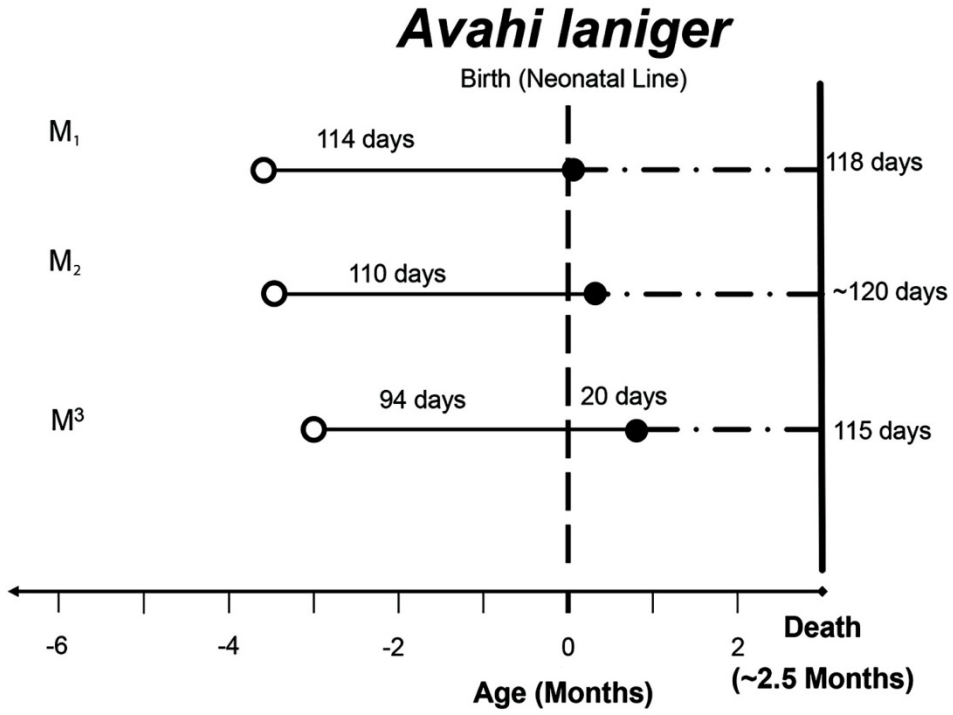


Figure 4.3. Molar chronology for Avahi laniger. The neonatal line was identified in all three molars analyzed in this study. Since the age at death was known for this individual (~2.5 months), the crown formation times, combined with root development data (not included), were used to cross-check the estimated age at death for this individual. Nearly the entire M_1 and M_2 crowns developed *in utero*, requiring 118 and ~120 days to form, respectively. There is a fracture in the cervical enamel of the M_2 and so the total crown formation time for the M_2 is an approximation; however, it highly likely that data for only a few days are not included in the estimation. There are limited data available on M^3 development in other taxa making comparisons difficult. The M^3 also develops mostly *in utero* and the crown is complete about 20 days after birth.

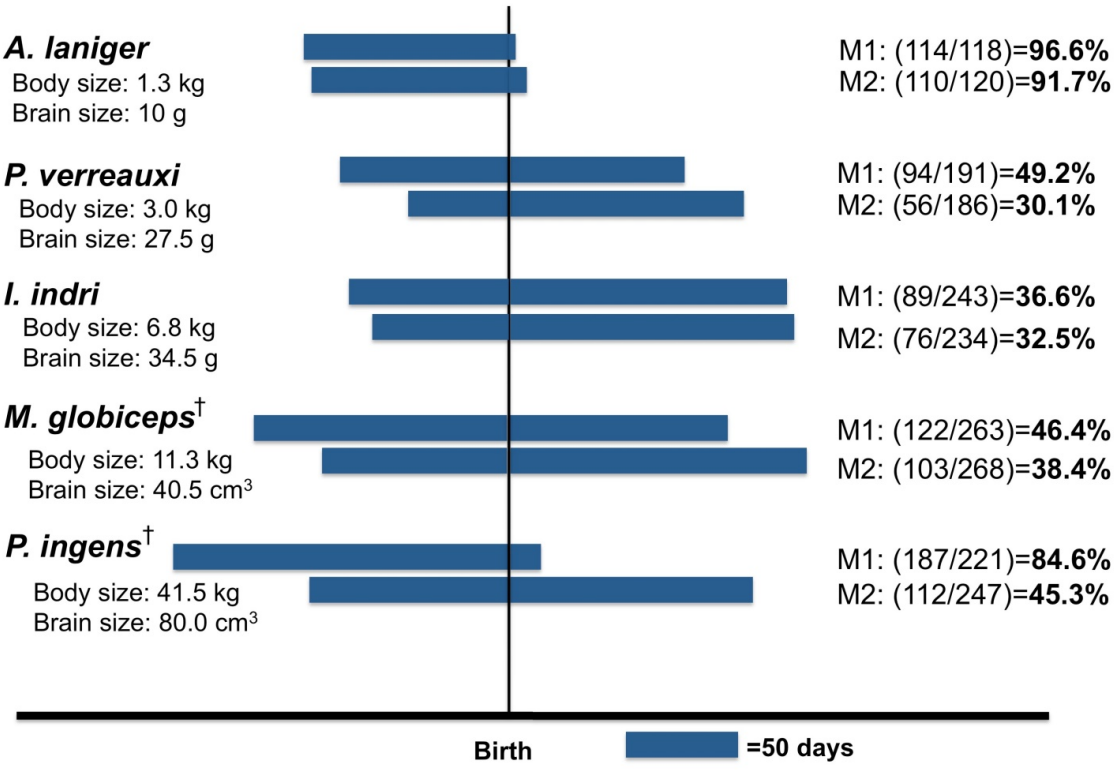


Figure 4.4. Comparisons of pre- and postnatal M1 and M2 crown development for the indriid- palaeopropithecid clade. The proportion of prenatal M1 and M2 of total crown formation times are reported as percentages. Body and brain sizes for each species are also included.

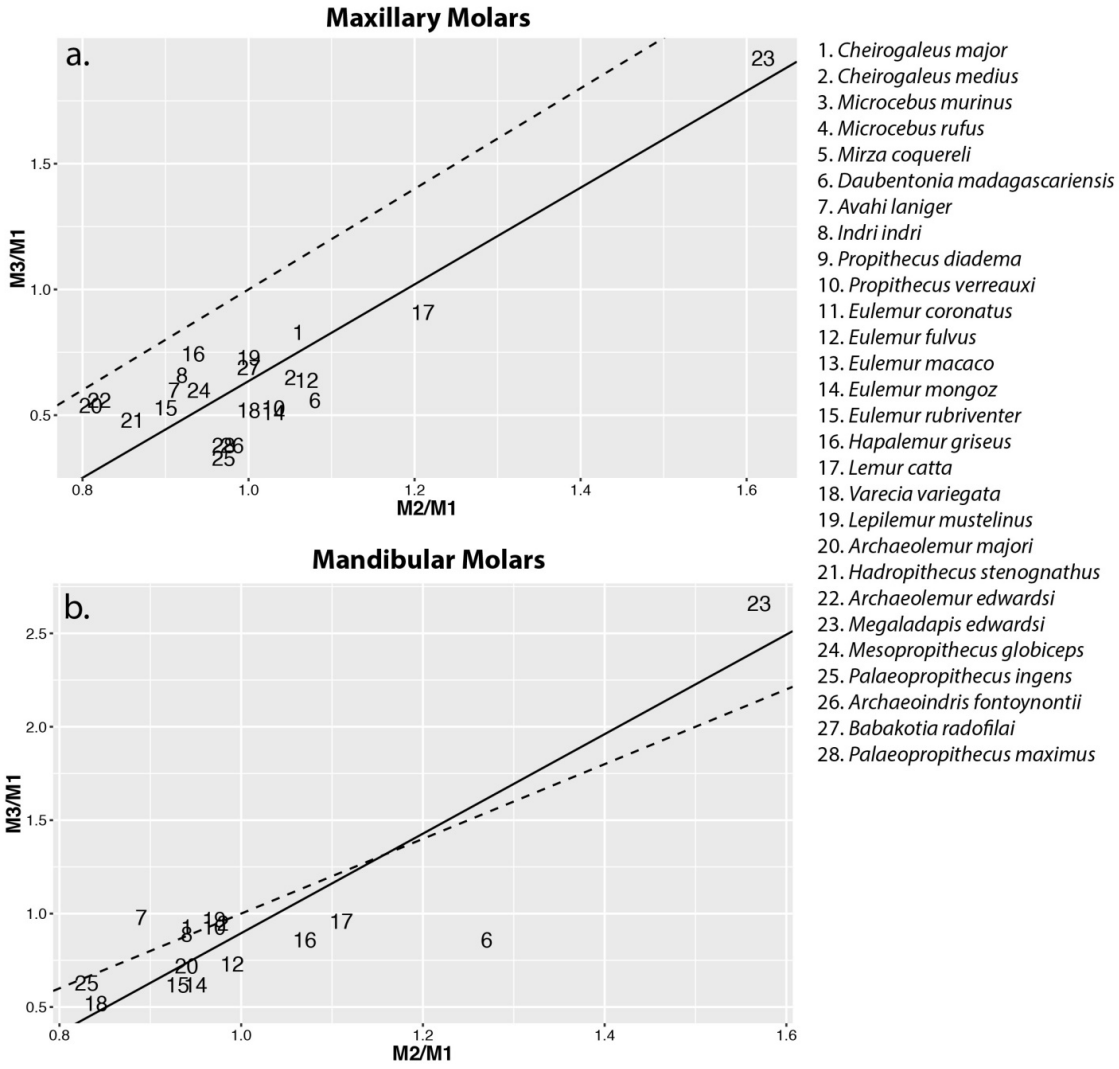


Figure 4.5a-b. RMA results for lemurs. The solid line represents the RMA results and the dotted line is the predicted line with a slope=2.0 and y-intercept = -1.0. Both arcades adhered to the expectations of the IC model; however, this appears to be primarily driven by *M. edwardsi* (see text for details). Representation of species for each arcade is based on available data.

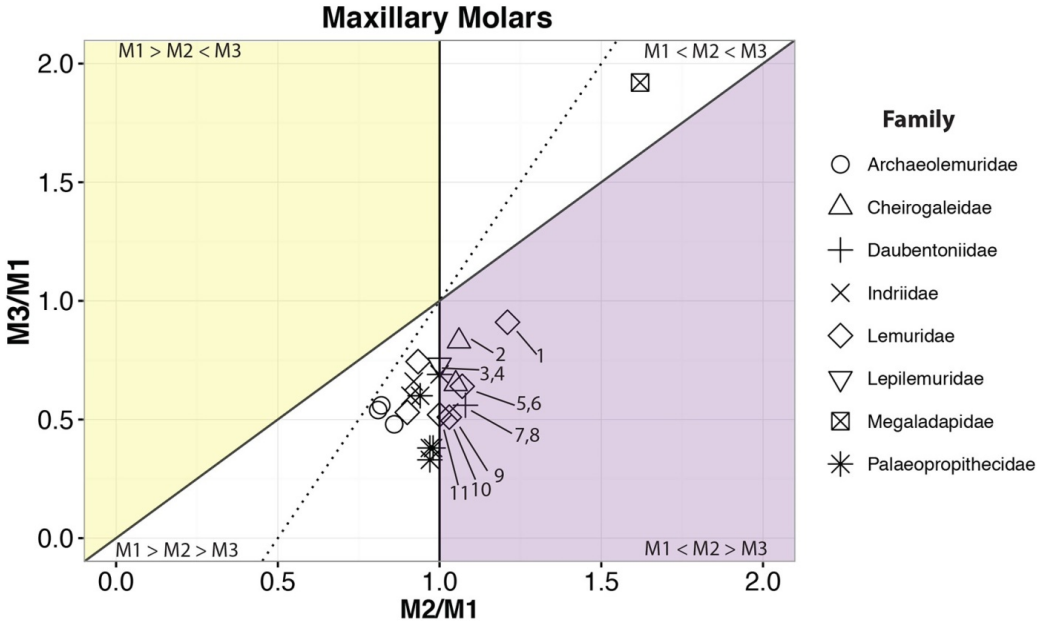


Figure 4.6. Maxillary molar proportions for extant and extinct lemurs (based on Polly's (2007) representation of the IC model as a "morphospace"). The white space represents where the molar row adheres to the linear expectations of the model and the dotted line is the original prediction (i.e., slope = 2.0, y-intercept = -1.0; Kavanagh et al., 2007). Areas in yellow (i.e., $M^1>M^2<M^3$) and purple (i.e., $M^1<M^2>M^3$) are spaces where the linear expectations of the model are not upheld. Several species did not adhere to the expectations of the model: 1) *Lemur catta* 2) *Cheirogaleus major* 3) *Cheirogaleus medius* 4) *Eulemur fulvus* 5) *Daubentonia madagascariensis* 6) *Propithecus verreauxi* 7) *Eulemur mongoz*. There were three species whose molar size sequence fell directly on the vertical 1.0 line (not labeled), where the M^1 and M^2 are approximately equal in area: *Lepilemur mustelinus* (Lepilemuridae), *Babakotia radofilai* (Palaeopropithecidae), and *Varecia variegata* (Lemuridae).

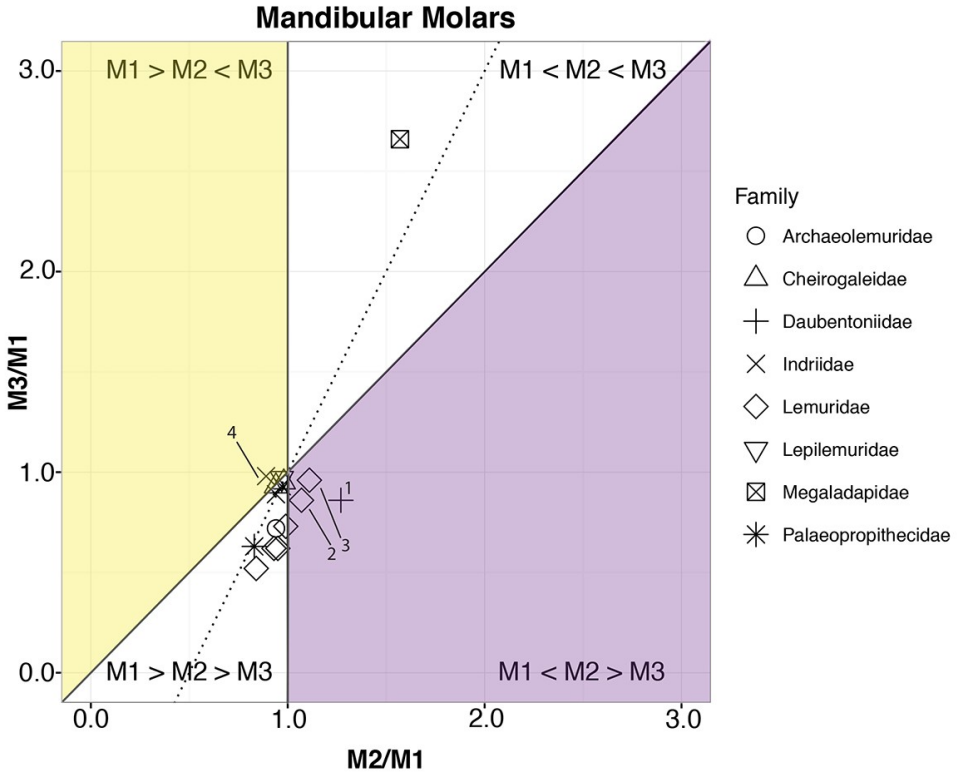


Figure 4.7. Mandibular molar proportions for extant and extinct lemurs (based on Polly's (2007) representation of the IC model as a "morphospace"). The white space represents where the molar row adheres to the linear expectations of the model and the dotted line is the original prediction (i.e., slope = 2.0, y-intercept = -1.0; Kavanagh et al., 2007). Areas in yellow (i.e., $M_1>M_2<M_3$) and purple (i.e., $M_1<M_2>M_3$) are spaces where the linear expectations of the model are not held. Several species did not adhere to the expectations of the model: 1) *Daubentonia madagascariensis* 2) *Hapalemur griseus* 3) *Lemur catta*, and 4) *Avahi laniger*.

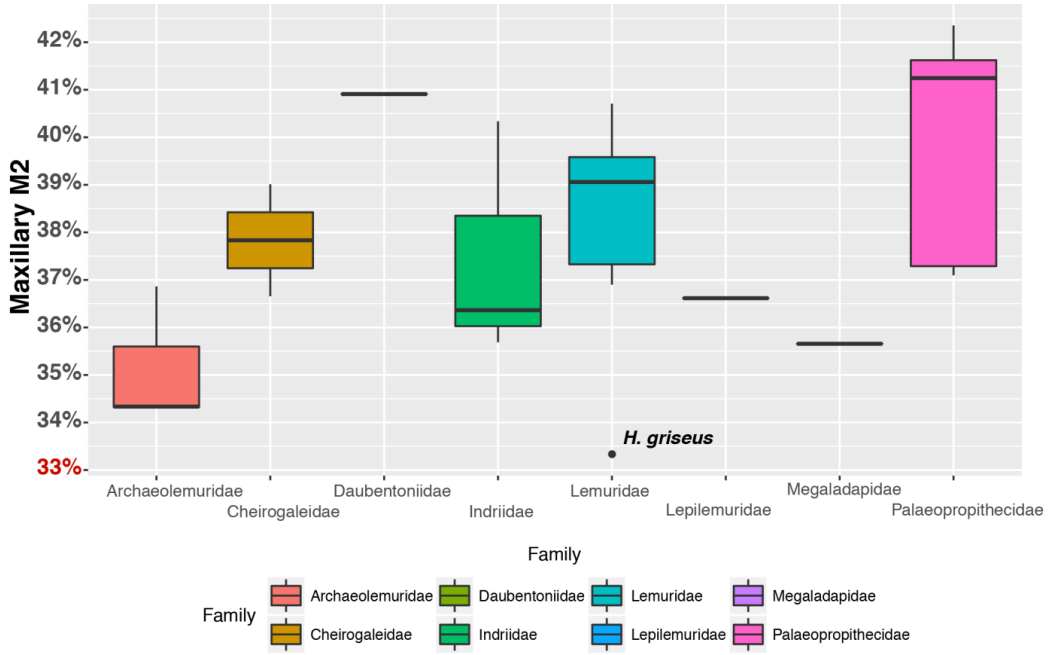


Figure 4.8. Box plot comparing the percentage M^2 comprises of the total molar area among lemur taxa. Nearly all of the lemur species have M^2s that comprise more than 33% of the total occlusal area, reflecting the trend for lemurs to have enlarged maxillary molars. Only *H. griseus* possesses M^2s that fit the prediction of the IC model.

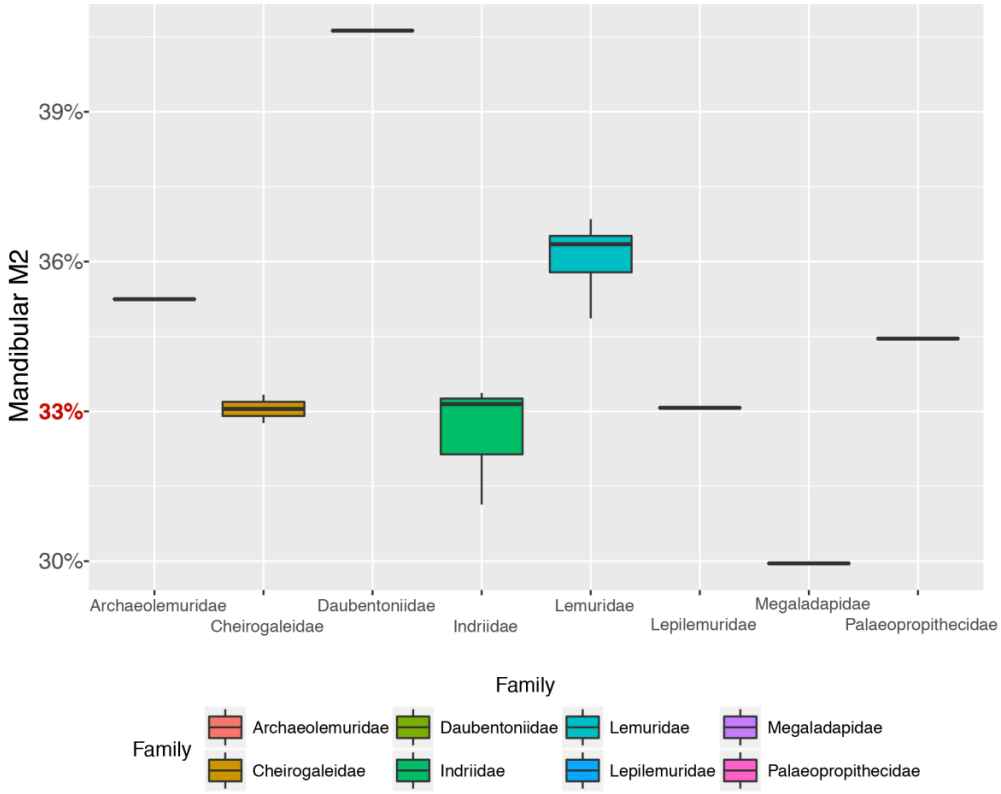
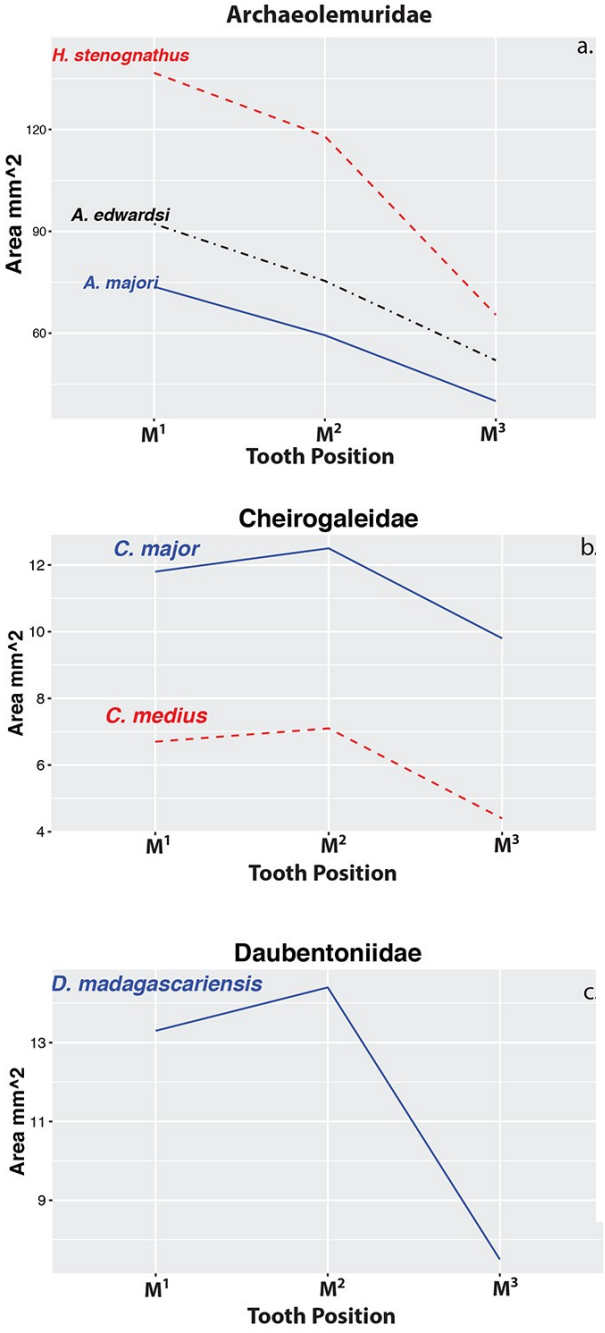
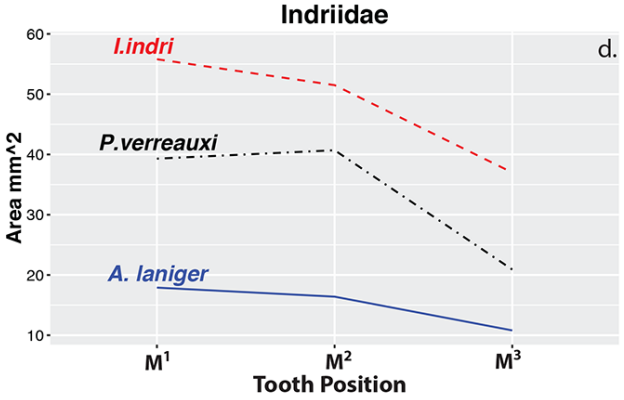
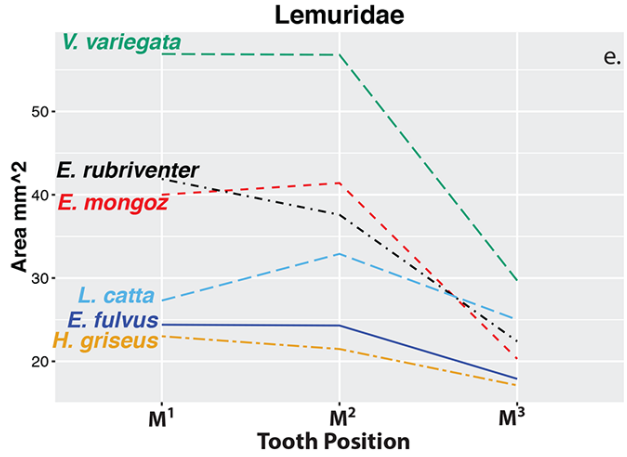


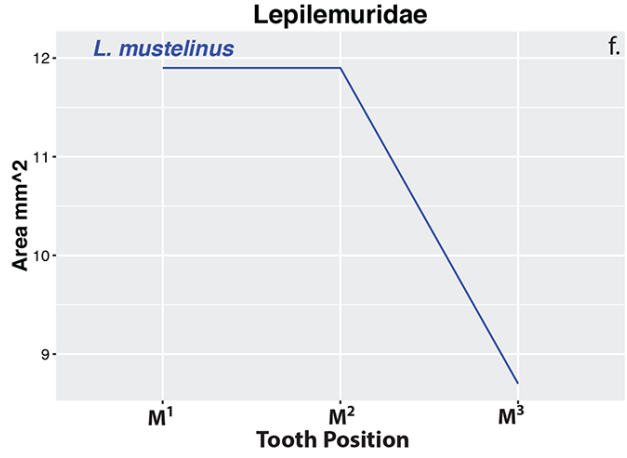
Figure 4.9. Box plot comparing the percentage M_2 comprises of the total molar area among lemur taxa. Species from the Cheirogaleidae, Indriidae, and Lepilemuridae families adhered to the prediction of the IC model, as these taxa fell on, or very close, to the predicted 33% mark. *M. edwardsi* fell below the 33% mark and the other taxa possess M_2s that occupy >33% of the total molar area.

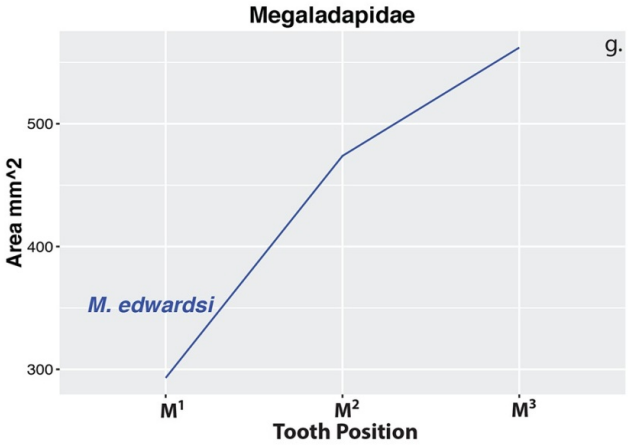


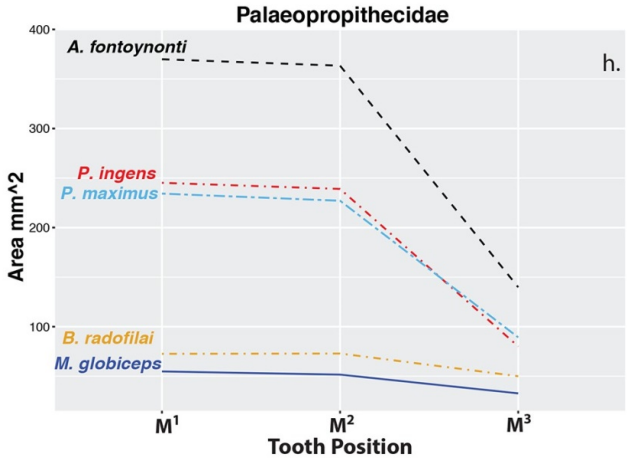
Figures 4.10a-h. Line graphs illustrating linear relationships of maxillary molar row for each species. None of the linear relationships are significant at the α-level of 0.05 (see text for details). Figure 4.10a. *A. edwardsi* (R^2=0.99, Adj. R^2=0.98, p-value=0.06); *A. majori* (R^2=0.99, Adj. R^2=0.98, p-value=0.055); *H. stenognathus* (R^2=0.93, Adj. R^2=0.859, p-value=0.171). Figure 4.10b. *C. major* (R^2=0.51, Adj. R^2=0.02, p-value=0.49); *C. medius* (R^2=0.63, Adj. R^2=0.25, p-value=0.42). Figure 4.10c. *D. madagascariensis* (R^2=0.62, Adj. R^2=0.25, p-value=0.42). Figure 4.10d. *A. laniger* (R^2=0.9, Adj. R^2=0.80, p-value=0.20); *I. indri*(R^2=0.91, Adj. R^2=0.82, p-value=0.19); *P. verreauxi*(R^2=0.29, Adj. R^2=0.39, p-value=0.37). Figure 4.10e. *E. fulvus* (R^2=0.76, Adj. R^2=0.52, p-value=0.32); *E. mongoz* (R^2=0.70, Adj. R^2=0.39, p-value=0.37); *E. rubiventer* (R^2=0.91, Adj. R^2=0.81, p-value=0.20); *H. griseus* (R^2= 0.93, Adj. R^2=0.86, p-value=0.18); *L. catta* (R^2=0.08, Adj. R^2=-0.84, p-value=0.82); *V. variegata* (R^2=0.76, Adj. R^2=0.51, p-value=0.33). Figure 4.10f. *L. mustelinus* (R^2=0.75, Adj. R^2=0.5, p-value=0.33). Figure 4.10g. *M. edwardsi* (R^2=0.96, Adj. R^2=0.92, p-value=0.12). Figure 4.10h. *A. fontoynonti* (R^2=0.77, Adj. R^2=0.54, p-value=0.32); *B. radofilai* (R^2=0.74, Adj. R^2=0.48, p-value=0.34); *M. globiceps* (R^2=0.86, Adj. R^2=0.71, p-value=0.25); *P. ingens* (R^2=0.78, Adj. R^2=0.56, p-value=0.31); *P. maximus* (R^2=0.79, Adj. R^2=0.57, p-value=0.31).

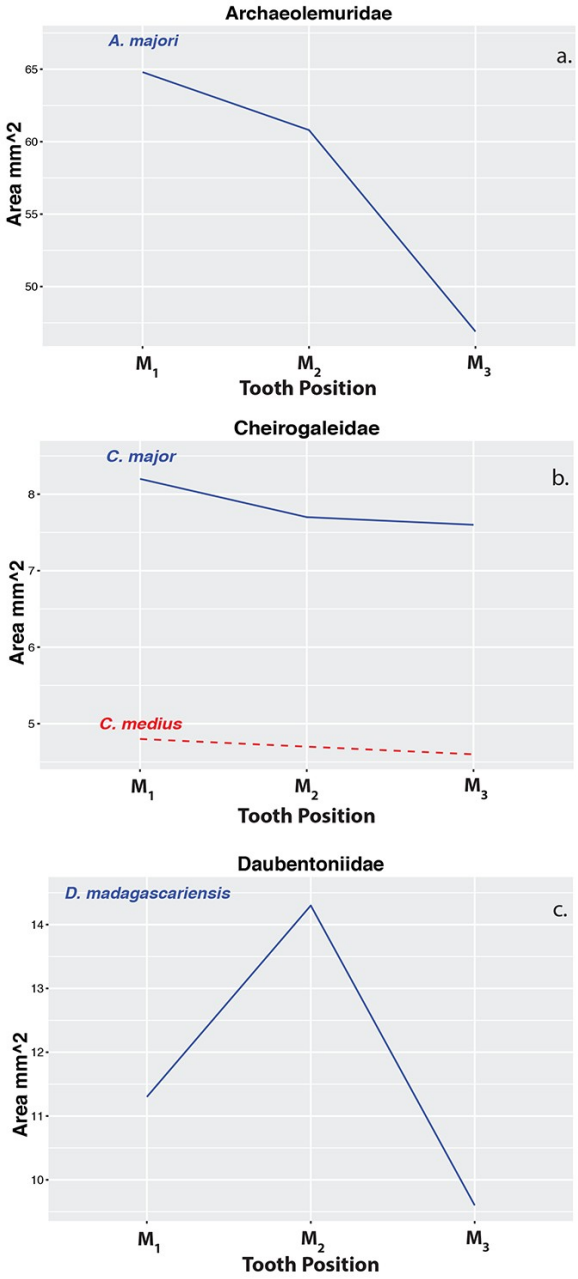

Indriidae
d.
I.indri
P.verreauxi
A. laniger
Area mm^2
60
50
40
30
20
10
M1
M2
M3
Tooth Position


Lemuridae
e.
V. variegata
E. rubriventer
E. mongoz
L. catta
E. fulvus
H. griseus
Area mm^2
50
40
30
20
M1
M2
M3
Tooth Position

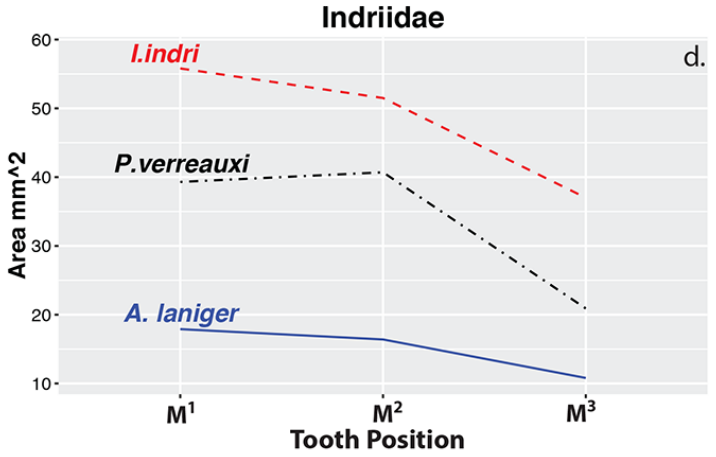

Lepilemuridae
f.
L. mustelinus
Area mm^2
12
11
10
9
M1
M2
M3
Tooth Position

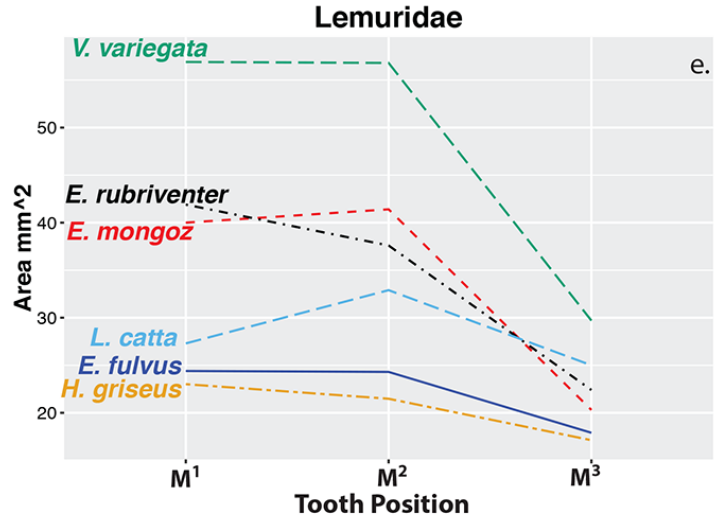

Megaladapidae
g.
500
400
300
Area mm^2
M. edwardsi
M1
M2
M3
Tooth Position

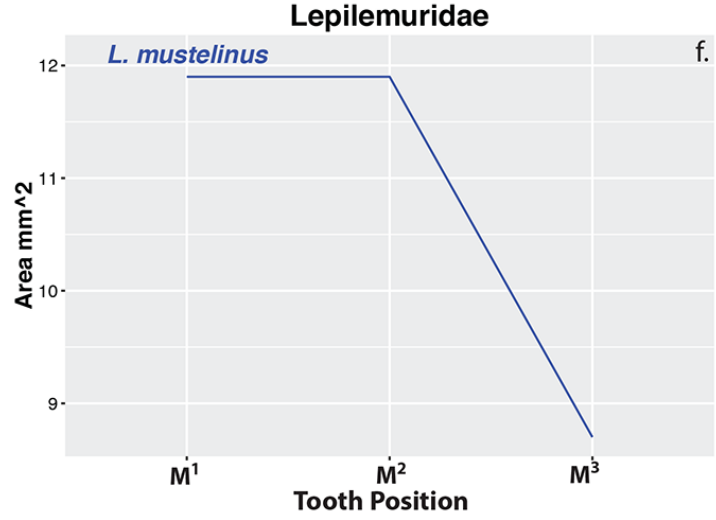

Palaeopropithecidae
h.
400
300
200
100
Area mm^2
A. fontoynonti
P. ingens
P. maximus
B. radofilai
M. globiceps
M1
M2
M3
Tooth Position

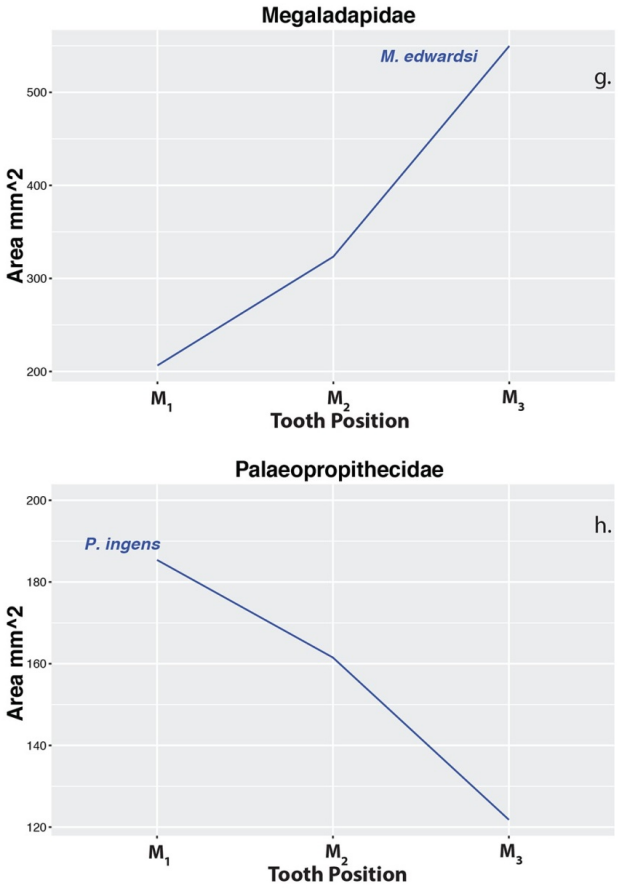


Figures 4.11a-h. Line graphs illustrating linear relationships of mandibular molar row for each species. Two of the linear relationships are significant at the α-level of 0.05(bolded; see text for details). Figure 4.11a. *A. majori* (R^2=0.91, Adj. R^2=0.81, p-value=0.20). Figure 4.11b. *C. major* (R^2=0.87, Adj. R^2=0.74, p-value=0.23); ***C. medius* ($R^2 \approx 1$, Adj. $R^2 \approx 1$, p-value <0.001.** Figure 4.11c. *D. madagascariensis* (R^2=0.13, Adj. R^2=-0.75, p-value=0.77); Figure 4.11d. *A. laniger* (R^2=0.04, Adj. R^2=-0.92; p-value=0.87); *I. indri* (R^2=0.99, Adj. R^2= 0.99, p-value=0.052); ***P. verreauxi* (R^2=0.99, Adj. R^2=0.99; p-value=0.02)**. Figure 4.11e. *E. fulvus* (R^2=0.61, Adj. R^2=0.22, p-value=0.43); *E. mongoz* (R^2=0.85; Adj. R^2=0.70, p-value=0.25); *E. rubiventer* (R^2=0.88, Adj. R^2= 0.76, p-value = 0.23); *H. griseus* (R^2=0.42, Adj. R^2=-0.17, p-value=0.55); *L. catta* (R^2=0.068, Adj. R^2=-0.83, p-value=0.83); *V. variegata* (R^2=0.96, Adj. R^2=0.92, p-value=0.12). Figure 4.11f. *L. mustelinus* (R^2=0.75, Adj. R^2=0.5, p-value=0.33). Figure 4.11g. *M. edwardsi* (R^2=0.99, Adj. R^2=0.98, p-value=0.06). Figure 4.11h. *P. ingens* (R^2=0.98, Adj. R^2=0.96, p-value=0.09).


Indriidae
d.
I.indri
P.verreauxi
A. laniger
Area mm^2
60
50
40
30
20
10
M1
M2
M3
Tooth Position


Lemuridae
e.
V. variegata
E. rubriventer
E. mongoz
L. catta
E. fulvus
H. griseus
Area mm^2
50
40
30
20
M1
M2
M3
Tooth Position


Lepilemuridae
f.
L. mustelinus
Area mm^2
12
11
10
9
M1
M2
M3
Tooth Position


Megaladapidae
M. edwardsi
g.
500
400
300
200
Area mm^2
M1
M2
M3
Tooth Position
Palaeopropithecidae
P. ingens
h.
200
180
160
140
120
Area mm^2
M1
M2
M3
Tooth Position

CHAPTER 5

CONCLUSIONS

Since Chapters 2-4 include their own discussion and conclusion sections, this chapter highlights possible broader avenues of future research based on the results of this dissertation project.

Summary and Future Research Directions

Reconstructing life history profiles of extinct primates, including hominins, enables researchers to test hypotheses about how and when the unusual modern human life history profile evolved (e.g., Bogin, 1999; Hill and Kaplan, 1999; Dean, 2010; Schwartz, 2012; Smith, 2013). Since a fundamental tenet of life history theory is to understand energetic trade-offs, reconstructed life history profiles provide an important guide for palaeobiologists to generate hypotheses on how extinct species mitigated mortality risks (e.g., bet-hedging; Roff, 2002; Godfrey and Rasoazanabary, 2012). While life history reconstructions offer a promising glimpse into the paleobiology of extinct species, and, by extension, insight into the evolution of life history, reconstructed life history profiles are still extremely limited for most extinct primates species. This is because paleoanthropologists are still refining methods (e.g., isotope analyses) and testing the usefulness of developmental patterns (e.g., M_1 emergence and its association to age at weaning) within various environmental contexts (e.g., unpredictable environments).

A key limitation for paleoanthropologists is that most life history data are not preserved in the fossil record (e.g., Robson and Wood, 2008). While biogeochemical analyses provide the best method to reconstruct absolute ages at weaning (e.g.,

Humphrey et al., 2008; Austin et al., 2013), most life history data for extinct species must be inferred from the developmental state of the preserved anatomy (e.g., Smith, 1992; Smith et al., 1995; Sardi and Ramirez-Rozzi, 2007; Dean and Cole, 2013). Therefore, this dissertation explored a number of topics all related to the broader goal of expanding our ability to reconstruct life history profiles and understand the evolution of life history in Primates.

Early weaning, slow pace of growth, and late age at reproduction are all part of a suite of energetic trade-offs that have shaped human evolution (Smith and Tompkins, 1995; Bogin, 1999; Hill and Kaplan, 1999; Robson and Wood, 2008). Since the development and emergence of the deciduous teeth coincide with some of these life history and growth parameters in great apes and humans, understanding how deciduous teeth wear in our closest living relatives may help inform paleoanthropologists about the evolution of human life history. Therefore, I tested hypotheses to assess whether there is evidence that the dp_4s wear in a manner that (presumably) preserve functional efficiency. I also assessed whether differences in dp_4 wear patterns were associated with weaning (i.e., the cessation of suckling) in great apes. Unfortunately, since known ages and ages at weaning are unknown for a large population of great ape species, it was not possible to test directly this hypothesis. Therefore, associations between dental wear and dental development relative to age at weaning were explored. While evidence exists that in most great ape species the dp_4s wear in a manner that maintains some aspect of the dental topography (Chapter 2), consistent associations between dp_4 wear and weaning were not found (Chapter 3). This suggests that the differential deciduous tooth wear, at least for the dp_4, is not a reliable marker for relative or absolute age at weaning.

Interestingly, early weaning, slow somatic growth, and late age at reproduction are also part of a suite of energetic trade-offs that have shaped the evolution of the indriid-palaeopropithecid clade. In contrast to hominins, the indriid-palaeopropithecid clade has extremely fast dental development and nearly vestigial deciduous teeth. Therefore, to gain insight into the evolution of the life history of the indriid-palaeopropithecid clade, I examined indriid molar development and applications of the inhibitory cascade (IC) model (a development-based model) in lemurs and compared growth and molar size data with life history variables (i.e., gestation length and age at weaning) (Chapter 4). Future research will examine relationships between tooth size and life history variables.

In Chapter 2, I quantified macrowear using dental topographic analyses in great ape dp_4s with the goal of establishing whether the occlusal surfaces wear in a manner that maintain dental topography. With the exception of *Pongo pygmaeus*, all the great ape species exhibited evidence of maintenance of dp4 dental topography, suggesting that dp_4s wear in a manner that maintain functional efficiency; however, the manner by which maintenance is achieved (e.g., preservation of complexity, preservation of relief) is species-specific. Interestingly, for *G. g. gorilla* and *P. t. schweinfurthii* there is evidence that the emergence of the M_2 seems to release some of the masticatory burden from the occlusal surfaces of the dp_4s, a pattern that does not appear in the other the great ape species.

Determining how diet affects occlusal macrowear is equally challenging because the precise mechanisms involved in tooth wear are still debated (reviewed in Chapter 1), but studies on the mechanical properties of foods is one of the most promising routes to

understand the causal mechanisms of tooth wear incurred from diet (e.g., Lucas, 2004). For example, in a wild population of *Theropithecus gelada*, Venkataraman et al. (2014) noted how younger individuals subsisted on foods with less challenging mechanical properties; however, in other primate species, such as *Sapajus libidinosus*, no differences in diet based on mechanical properties between adults and juveniles were observed (Chalk et al., 2016). Extending a similar research program to the great apes may provide additional insight into the deciduous tooth wear patterns reported in this dissertation, and, by extension, shed light on the differential wear observed on the deciduous dentition in hominins. In order to apply such data to a life history framework, it is also important to assess how such information would relate to growth and development. Therefore, it is recommended to record mechanical properties data alongside caloric and nutritional data for foods ingested (e.g., individual plants and plant parts), especially by juveniles. Such an approach could provide a model to categorize foods on a scale of their energetic costs and benefits, rather than just on the mechanical properties alone (e.g., Norconk et al., 2009; Lambert and Rothman, 2015).

In Chapter 3, this project tested whether differences in dp_4 wear among closely related species, in this case the great apes, could be attributed to age at weaning (Aiello et al., 1991). The results of this study found little to no evidence that differences in age at weaning can be attributed to macrowear differences on the dp_4. Chapter 3 discusses different research directions, including the possibility of testing this hypothesis on the anterior dentition, where, perhaps, more extreme wear differences among great apes species have been observed (Aiello et al. 1991). Since 1991, studies on wild populations of great apes have greatly increased in number and more data are now available to assess

the variation in age at weaning within great ape species (reviewed in Chapter 3). A broader issue that needs consideration is the tremendous overlap in age at weaning among the great ape species and whether the apes provide a good model to predict age at weaning in hominins (e.g, Kelley and Schwartz, 2012; Schwartz, 2012; Smith, 2013).

Although partially destructive, biogeochemical analyses of a few hominin teeth representing different species would be able to inform paleoanthropologists what age hominin species were weaned (e.g., Austin et al., 2013). Such a study would provide key life history data to resolve the debate about *when* early weaning evolved and shed light on the evolution of cooperative breeding strategies (i.e., alloparenting) in hominins. Still, more than biogeochemical data are needed. Absolute ages at death and rates of dental development will continue to provide necessary growth and development data to calibrate other aspects of somatic growth (e.g., skeletal growth) to reconstruct hominin life history profiles (e.g., Dean and Cole, 2013). Perhaps, one day, growth rate differences that coincide with preserved chemical signatures of hormonal fluctuations preserved in fossils (e.g., bone, enamel, or fossilized calculus) will enable paleoanthropologists to determine the absolute sex and/or the onset of puberty in primates, including hominins. Such data might provide information about other important aspects of life history profiles (e.g., age at first reproduction) beyond age at weaning.

Despite the lack of association between dp_4 wear and weaning in great apes, several interesting dental developmental patterns relative to age at weaning surfaced in this dissertation. Interestingly, M_2 emergence, not just M_1 emergence, overlaps with weaning in a number of different great ape species, suggesting that further exploration of possible associations between M_2 emergence and weaning is warranted for great apes.

Likewise, comparisons among different great ape populations that assess variation between molar emergence and age at weaning are also fruitful avenues to explore the relationship between dental development and weaning (e.g., Zihlman et al., 2004; Smith et al., 2013).

Paleoanthropologists have noted that in humans and chimpanzees (i.e., *P. t. schwwinfurthii*) there is a complete dissociation between age at weaning and M_1 emergence. In chimpanzees, M_1 emerges *before* age at weaning and in humans M_1 emerges *after* age at weaning (Chapter 3, citations therein). Perhaps, a broad comparative study (primates and other non-mammalian primates) that explore under what conditions (e.g., environmental) age at weaning and M_1 are dissociated in other mammals may shed light on the dissociation of M_1 development and weaning in hominins.

Finally, Chapter 4 provides dental developmental data that can be used to reconstruct life history profiles in extinct species of lemurs. Since most lemurs are seasonal breeders that engage in synchronous weaning, set life history parameters are already in place to figure out the timing of life history events using dental development (e.g., Schwartz et al., 2002; Catlett et al., 2010). In this chapter, new data are presented and confirm that the indriid-palaeopropithecid clade exhibits extremely fast dental development. For example, the molar chronologies for *A. laniger* reveal that the timing of initiation in the M_2 is only four days after the initiation of M_1. Interestingly, the smallest bodied lemur in this clade (*Avahi*) and the largest member for which there are data (*Palaeopropithecus*) share similar proportions of M1 development *in utero*. Correlation assessments suggested that neither body nor brain size were associated with the pace of molar crown development in this clade.

This chapter also assesses whether lemurs adhered to the IC model. The results were mixed and only data for molars were considered. Future research that includes the deciduous premolars would strengthen the study to ascertain how lemurs may (or may not) adhere to this developmental mechanism. Interestingly, the size of the M_2 had the highest significant Pearson correlation coefficients with body size, brain size, and age at weaning. Future research in other primate groups (e.g., haplorhines) that explore whether the size of the M_2 correlates with life history or life history-related variables (i.e. body and brain size) may provide another avenue to reconstruct aspects of life history profiles. If the size of molars affect fitness, even indirectly, (e.g., Degusta et al., 2003), then the reoccurrence of the M_2 as a potentially influential tooth in this dissertation suggests additional future research possibilities. For example, in *G. g. gorilla* and *P. t. schweinfurthii*, the presence of the M_2 appears to influence dp_4 wear patterns (Chapter 2). M_2 emergence seems to coincide with weaning for several great ape species (Chapter 3). In lemurs, the size of the M_2 correlates with age at weaning and initiates early in comparison to other primates (Chapter 4). Given the reoccurring importance of the M_2 in this dissertation, along with its developmental connection with the formation of the primary postcanine dentition, it is possible that selection for differences in M_2 size will produce different activator/inhibitor ratios that should be reflected in different primary postcanine dental proportions and, possibly, might be associated with variation in life history profiles.

References

Austin, C., Smith, TM., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D. , Hare, D.J., Doble, P., Eskenazi, B. Arora, M. 2013. Barium distributions in teeth reveal early-life dietary transitions in primates. Nature 498:216-219.

Bogin, B. 1999. Evolutionary perspective on human growth. Annu Rev Anthropol 28:109-153.

Catlett, KK., Schwartz, GT., Godfrey, LR. Jungers, WL. 2010. "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. Am J Phys Anthropol 142:391-404.

Chalk, J., Wright, BW., Lucas, PW., Schuhmacher, KD., Vogel, ER., Fragaszy, D., Visalberghi, E., Izar, P., Richmond, B. 2016. Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. Am J Phys Anthropol 159:199-209.

Dean, MC. 2010. Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. Phil Trans R Soc Lond B 365:3397-3410.

Dean, MC., Cole, TJ. 2013. Human life history evolution explains dissociation between the timing of tooth eruption and peak rates of root growth. PLOS One 8:1-14.
Degusta, D., Everett, MA. Milton, K. 2003. Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). Proc Biol Sci 270 Suppl 1:S15-7.

Godfrey, LR., Rasoazanabary, E. 2012. Demise of the bet hedgers: A case study of human impacts on past and present lemurs of Madagascar. In: Sodikoff, G. M., editor. The Anthropology of Extinction: Essays on Culture and Species Death. pp 165–199.

Hill, K., Kaplan, H. 1999. Life history traits in humans: Theory and empirical studies. Ann Rev Anthropol 28:397-430.

Humphrey, L., Dirks, W., Dean, C. Jeffries. 2008. Tracking dietary transitions in weanling baboons (*Papio hamadryas anubis*) using strongtium/calcium ratios in enamel. Folia Primatol 79:197-212.

Kelley, J., Schwartz, GT. 2012. Life-history inference in the early hominins *Australopithecus* and *Paranthropus*. Int J Primatol 1-32.

Lambert, JE., Rothman, JM. 2015. Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. Annu Rev Anthropol 44:493-512.

Lucas, PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: CambridgeUniversity Press.

Norconk, MA., Wright, BW., Conklin-Brittain, NL. Vinyard, C. J. 2009. Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garger, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. W. Strier, K. B. et al., editors. South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation. Springer. pp 279–319.

Robson, SL., Wood, B. 2008. Hominin life history: Reconstruction and evolution. J Anat 212:394-425.

Roff, DA. 2002. Life history evolution. Sunderland, Massachusetts: Sinauer Associates, Inc.

Sardi, M. L., Ramirez-Rozzi, F. 2007. Developmental connections between cranial components and the emergence of the first permanent molar in humans. J Anat 210:406-417.

Schwartz, GT. 2012. Growth, development, and life history throughout the evolution of *Homo*. Curr Anthrolpol 53:S395-S408.

Schwartz, GT, Samonds, KE, Godfrey, LR, Jungers, WL, Simons, EL. 2002. Dental microstructure and life history in subfossil Malagasy lemurs. Pro Natl Acad Sci, USA 99 (9): 6124–29.

Smith, BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:134-142.

Smith, RJ., Gannon, PJ. Smith, BH. 1995. Ontogeny of australopithecines and early *Homo* - evidence from cranial capacity and dental eruption. J Hum Evol 29:155-168.

Smith, TM. 2013. Teeth and human life-history evolution. Annu Rev Anthropol 42:191-208.

Smith, BH., Tompkins, RL. 1995. Toward a life-history of the hominidae. Ann Rev Anthropol 24:257-279.

Venkataraman, VV, Glowacka, H, Fritz, J, Clauss, M, Seyoum, C, Nguyen, N, Fashing, PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155 (1): 17–32.

REFERENCES

Aiello, LC, Montgomery, C, Dean, MC. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397–412.

Ali, JR., Huber, M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. Nature 463:653-656.

Altmann, SA. 1991. Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proc Natl Acad Sci USA 88:420–23.

Alqahtani, SJ., Hector, MP. Liversidge, HM. 2014. Accuracy of dental age estimation charts: Schour and Massler, Ubelaker and the London atlas. Am J Phys Anthropol 154:70-78.

Ankel-Simons, F. 2007. An introduction to primate anatomy. San Diego: Academic Press.

Antoine, D., Hillson, S. Dean, MC. 2009. The developmental clock of dental enamel: A test for the periodicity of prism cross-striations in modern humans and an evaluation of the most likely sources of error in histological studies of this kind. J Anat 214:45-55.

Asahara, M. 2013. Unique inhibtory cascade pattern of molars in canids contributing their potential to evolutionary plasticity of diet. Evol Evol 3:278-285.

Ashton, EH., Zuckerman, S. 1950. Some quantitative dental characteristics of the chimpanzee, gorilla and orang-outang. Philos T R Soc B 234:471-484.

Atsushi, Y, Uasui, K, Sonomura, T., Iwai, H., Uemura, M. 2010. Development of deciduous and permanent dentitions in the upper jaw of the house shrew (*Suncus murinus*). Arch Oral Biol 55(4): 279–287.

Austin, C., Smith, TM., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D. , Hare, D.J., Doble, P., Eskenazi, B. Arora, M. 2013. Barium distributions in teeth reveal early-life dietary transitions in primates. Nature 498:216-219.

Baker, G., Jones, L. H. P. Wardrop, I. D. 1959. Cause of wear in sheeps' teeth. Nature 184:1583-1584.

Barrickman, NL., Lin, MJ. 2010. Encephalization, expensive tissues, and energetics: An examination of the relative costs of brain size in strepsirrhines. Am J Phys Anthrpol 143:579-590.

Bartoń, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. https://CRAN.R-project.org/package=MuMIn

Bateson, P. 1994. The dynamics of parent-offspring relationships in mammals. Trends Ecol Evol 9:399-403.

Baume, LJ. 1950. Physiological tooth migrations and its significance for the development of occlusion: I. The biogenetic course of the deciduous dentition. J of Dent Res 29:123-132.

Bayne, K., Turner, PV. 2014. Animal environments and their impact on laboratory animal welfare. In: Bayne, K., Turner, PV. pp 77–94.

Bernal, V., And Gonzalez, PN. And Perez, SI. 2013. Developmental processes, evolvability, and dental diversification of New World Monkeys. Evol Biol 40:532-541.

Berkovitz, B., Moxham, BJ., Linden, R. Sloan, A. 2011. Master Dentistry (Volume 3). Edinburgh: Elsivier.

Berthaume, MA. 2016. Food mechanical properties and dietary ecology. Am J Phys Anthropol 159:79-104.

Berthaume, MA., Dumont, ER., Godfrey, LR. Grosse, IR. 2013. How does tooth cusp radius of curvature affect brittle food item processing? J R Soc Interface Journal of the Royal Society Interface 10:20130240.

Beynon, AD., Dean, MC. Reid, DJ. 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. Am J Phys Anthropol 86:189-203.

Birch, W., Dean, C. 2009. Rates of enamel formation in human deciduous teeth. Front Oral Biol 13:116-120.

Blanco, MB., Godfrey, LR. 2013. Does hibernation slow the ”pace of life in dwarf lemurs (*Cheirogaleus spp.*)? Int J Primatol 34:130-147

Bogin, B. 1999. Evolutionary perspective on human growth. Annu Rev Anthropol 28:109-153.

Borries, C., Gordon, AD. Koenig, A. 2013. Beware of primate life history data: a plea for data standards and a repository. PLOS One 8:1-12.

Borrero-Lopez, O, Pajares, A., Constantino, PJ, Lawn, BR. 2014. A model for predicting wear rates in tooth enamel. J Mech Behav Biomed Mater 37:226–34.

Boughner, JC., Dean, MC., Wilgenbusch, CS. 2012. Permanent tooth mineralization in bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*). Am J Phys Anthropol 149:560-571.

Boyer, DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol. 55 (6): 1118–37.

Britton, K., Fuller, BT., Tüken, T., Mays, S., Richards, MP. 2015. Oxygen isotope analysis of human bone phosphate evidences weaning age in archaeological populations. Am J Phys Anthropol 157:226-241.

Breuer, T., Hockemba, MB., Olejniczak, C., Parnell, RJ. Stokes, EJ. 2009. Physical maturation, life-history classes and age estimates of free-ranging western gorillas-insights from Mbeli Bai, Republic of Congo. Am J Primatol 71:106-119.

Bromage, TG. 1991. Enamel incremental periodicity in the pig-tailed macaque: A polychrome fluorescent labeling study of dental hard tissues. Am J Phys Anthropol 86:205-214.

Bromage, TG., Lacruz, RS., Hogg, R., Goldman, HM., Mcfarlin, SC., Warshaw, J., Dirks, W., Perez-Ochoa, A., Smolyar, I., Enlow, DH., Boyd, A. 2009. Lamellar bone is an incremental tissue reconciling enamel rhythms, body size, an organismal life history. Calcif Tissue Int 84:388-404.

Bullington, J. 1991. Deciduous dental microwear of prehistoric juveniles from the lower Illinois River Valley. Am J Phys Anthropol 84:59-73.

Bunn, JM, Ungar, PS. 2009. Dental topography and diets of four Old World monkey species. Am J Primatol 71(6): 466–77.

Bunn, JM., Boyer, DM., Lipman, Y., St Clair, EM., Jernvall, J. Daubechies, I. 2011. Comparing Dirichlet Normal Surface Energy of tooth crowns, a new technique of molar Shape quantification for dietary inference, with previous methods in isolation and in Combination. Am J Phys Anthropol 145:247-261.

Burkart, JM., Hrdy, SB. van Schaik, CP 2009. Cooperative breeding and human cognitive evolution. Evol Anthropol 18:175-186.

Burney, DA., Burney, LP., Godfrey, LR., Jungers, WL., Goodman, SM., Wright, HT., Jull, AJT. 2004. A chronology for late prehistoric Madagascar. J Hum Evol 47:25-63.

Burnham, K. P., Anderson, DR. 2002. Model section and multimodel inferences: a practical information-theoretic approach (2 ed.). New York: Springer.

Burns, SJ., Godfrey, LR., Faina, P., Mcgee, D., Hardt, B., Ranivoharimanana, L., Randrianasy, J. 2016. Rapid human-induced landscape transformation in Madagascar at the end of the first millennium of the common era. Quaternary Science Reviews 134:92-99.

Catlett, KK., Schwartz, GT., Godfrey, LR. Jungers, WL. 2010. "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. Am J Phys Anthropol 142:391-404.

Carlson, BA., Kingston, JD. 2014. Chimpanzee isotopic ecology: A closed canopy C_3 template for hominin dietary reconstruction. J Hum Evol 76:107 - 115.

Cerling, TE., Chritz, KL., Jablonski, NG., Leakey, MG. Manthi, FK. 2013. Diet of *Theropithecus* from 4 to 1 ma in Kenya. Proc Natl Acad Sci 110:10507-10512.

Chai, H., Lee, JJ., Constantino, PJ., Lucas, PW. Lawn, BR. 2009. Remarkable resilience of teeth. Proc Natl Acad Sci USA 106:7289-7293.

Chalk, J., Wright, BW., Lucas, PW., Schuhmacher, KD., Vogel, ER., Fragaszy, D., Visalberghi, E., Izar, P., Richmond, B. 2016. Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. Am J Phys Anthropol 159:199-209.

Charnov, EL., Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. Evol Anth 1:191-194.

Clark, CB. 1977. A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In: Skolnikoff, C., Poirier, FE., eds. Primate bio-social development: biological, social, and ecological determinants. New York: Garland. pp. 235–260.

Clementz, MT. 2012. New insight from old bones: Stable isotope analysis of fossil mammals. J Mammal 93:368-380.

Conolly, J., Lake, M. 2012. Geographical information systems in Archaeology. Cambridge: Cambridge University Press.

Conover, WJ., Iman, RL. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124-129.

Conover, WJ. 2012. The rank transformation-an easy and intuitive way to connect many nonparametric methods to their parametric counterparts for seamless teaching introductory statistics courses. Computation Stat 4:432-438.

Constantino, PJ., Lee, J.J.W., Gerbig, Y., Hartstone-Rose, A., Talebi, M., Lawn, BR. 2012. The role of tooth enamel mechanical properties in primate dietary adaptation. Am J Phys Anthropol 148:171-177.

Copes, LE., Schwartz, GT. 2010. The scale of it all: Postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law. Paleobiology 36:188-203.

Constantino, PJ., Wright, BW. 2009. The importance of fallback foods in primate ecology and evolution. Am J Phys Anthropol 140:599-602.

Crowley, BE. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quatern Sci Rev 29:2591-2603.

Cuozzo, FP., Sauther, ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. J Hum Evol. 51:490-505.

Cuozzo, F. P., Sauther, ML. 2012. What is dental ecology? Am J Phys Anthropol 148:163-170.

Cuozzo, FP., Ungar, PS. Sauther, ML. 2012. Primate dental ecology: How teeth respond to the environment. Am J Phys Anthropol 148:159-162.

Dale, P. 2005. Introduction to Mathematical Techniques used in GIS. Boca Raton: CRC Press.

Daly, ES and Catlett, KK. 2014. A test of inhibitory cascade (IC) model on primate deciduous premolars. Am J Phys Anthropol Suppl 58:102.

Daly, ES, Catlett, KK, Paul, KS, Nesse, HP. 2015.An intraspecific analysis of the inhibitory cascade (IC) model in gorillas, chimpanzees, and modern humans. Am J Phys Anthropol Suppl. 60:115.

Daniel, WW. 2000. Applied nonparametric statistics (2nd ed.). Pacific Grove, CA: Duxbury Thompson Learning.

Darnell, LA., Teaford, MF, Livi, KJT, Weihs, TP. 2010. Variations in the mechanical properties of *Alouatta palliata* molar enamel. Am J Phys Anthropol 141 (1): 7–15.

Dart, RA. 1925. *Australopithecus africanus*: The man-ape of South Africa. Nature 195-199.

Dart, RA. 1948. The adolescent mandible of *Australopithecus prometheus.* Am J Phys Anthropol 6:391-412.

Dean, MC. 1993. Daily rates of dentine formation in macaque tooth roots. Int J Osteoarchaeol 3:199-206.

Dean, MC. 1995. The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 (*Homo habilis*). In: Moggi-Cecchi, J., editor. Aspects of Dental Biology: Paleontology, Anthropology, and Evolution. Florence: International Institute for the Study of Man. pp 239–265.

Dean, MC. 2010. Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. Phil Trans R Soc Lond B 365:3397-3410.

Dean, MC., Cole, TJ. 2013. Human life history evolution explains dissociation between the timing of tooth eruption and peak rates of root growth. PLOS One 8:1-14.

Dean, MC., Leakey, MG. 2004. Enamel and dentine development and the life history profile of *Victoriapithecus macinnesi* from Maboko Island, Kenya. Annals of Anatomy 186:405-412.

Dean, MC, Wood, BA. 1981. Developing pongid dentition and its use for aging individual crania in comparative cross-sectional growth studies. Folia Primatol 36 (1-2): 111–27.

Dean, MC., Beynon, AD., Reid, DJ. Whittaker, DK. 1993. A longitudinal study of tooth growth in a single individual based on long-and short-period incremental markings in dentine and enamel. Int J Osteoarchaeol 3:249-264.

Dean, C., Leakey, MG., Reid, D., Schrenk, F., Schwartz, GT., Stringer, C. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414:628-631.

Degusta, D., Everett, MA. Milton, K. 2003. Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). Proc Biol Sci 270 Suppl 1:S15-7.

Delezene, LK., Kimbel, WH. 2011. Evolution of the mandibular third premolar crown in early *Australopithecus.* J Hum Evol 60:711-730.

Delgado, RA., van Schaik, CP. 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. Evol Anthropol 9:201-218.

Dennis, JC, Ungar, PS, Teaford, MF, Glander, KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125 (2): 152–61.

Dettwyler, KA. 1995. A time to wean the hominind bluprint for the natural age of weaning in modern human populations. In: Stuart-Macadam, P, Dettwyler, KA., editors. Breastfeeding: biocultural perspectives. New York: Aldine de Gruyter. pp 39–73.

Dettwyler, KA. 2004. When to wean: biological versus cultural perspectives. Clin Obstet Gynecol 47:712-723.

Dewar, RE., Richard, AF. 2007. Evolution in the hypervariable environment of Madagascar. Proc Natl Acad, USA 104:13723-13727.

Dirks, W. 2003. Effect of diet on dental development in four species of catarrhine primates. Am J Primatol 61:29-40.

Dirks, W., Humphrey, LT., Dean, MC. Jeffries, TE. 2010. The relationship of accentuated lines in enamel to weaning stress in juvenile baboons (*Papio hamadryas anubis*). Folia Primatol 81:207-223.

Douglass, K., Zinke, J. 2015. Forging ahead by land and by sea: archaeology and paleoclimate reconstruction in Madagascar. Afr Archaeol Rev 32:267-299.

Eaglen, RH. 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. Am J Phys Anthropol 66:307-315.

Elgart, AA. 2010. Dental wear, wear rate, and dental disease in the african apes. Am J of Primatol 71:1–11.

Evans, AR. 2013. Shape descriptors as ecometrics in dental ecology. Hystrix: the Italian Journal of Mammalogy 24:133-140.

Evans, AR., Janis, CM. 2014. The evolution of high dental complexity in the horse lineage. Ann Zool Fennici 51:73-79.

Evans, AR., and Jernvall, J. 2009. Patterns and constraints in carnivoran and rodent dental complexity and tooth size. J Vert Paleo 29 24A.

Evans, AR, Wilson, GP, Fortelius, M, Jernvall, J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445: 78–81.

Evans, AR, Daly, ES, Catlett, KK, Paul, KS, King, SJ, Skinner, MM, Nesse, HP, Hublin, JJ, Townsend, GC, Schwartz, GT, Jernvall, J. 2016. A simple rule governs the evolution and development of hominin tooth size. Nature 530: 477-480.

Field, A. 2009. Discovering Statistics Using SPSS. Los Angeles: Sage.

Fitzgerald, C., Saunders, S., Bondioli, L. Macchiarelli, R. 2006. Health of infants in an imperial roman skeletal sample: Perspective from dental microstructure. Am J Phys Anthropol 130:179-189.

Flanagan, EK. 2004. The ontogeny of dental use wear in *Archaeolemur* spp. and *Macaca fascicularis*. University of Massachusetts. Master's Thesis.

Fleagle, JG. 2013. Primate Adaptations and Evolution. London: Academic Press.

Fletcher, AW. 2001. Development of infant independence from the mother in the wild mountain gorillas. In: Robbins, MM., Sicotte, P. Stewart, KJ. et al., eds. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 153–183.

Fossey, D. 1979. Development of the mountain gorilla (*Gorilla gorilla beringei*): The first 36 months. Perspect Hum Evol 5:139-184.

Galbany, J, Altmann, J, Perez-Perez, A, Alberts, SC. 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. Am J Phys Anthropol 144 (1): 51–59.

Galbany, J., Imanizabayo, O., Romero, A., Vecellio, V., Glowacka, H., Cranfield, MR., Bromage, TG, Mudakikwa, A., Stoinski, TS, and McFarlin, S. 2016. Tooth wear and feeding ecology in mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol. Early View.

Galbany J, Romero A, Mayo-Alesón M, Itsoma F, Gamarra B, Pérez-Pérez A, Willaume E, Kappeler PM, Charpentier MJE. 2014. Age-related tooth wear differs between forest and savanna primates. PLoS One 9:e94938.

Ganzhorn, JU. 1995. Cyclones over Madagascar: fate or fortune. Ambio 24:125-124.

Gingerich, PD., Smith, BH. Rosenberg, K. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. Am J Phys Anthropol 58:81-100.

Gipps, JM, Sanson, GD. 1984. Mastication and digestion in *pseudocheirus*. In: Smith, AP and Hume, ID, editors. Possums and gliders. Sydney: Australian Mammal Society, p. 237–246.

Glowacka, H, McFarlin, S., Catlett, KK., Mudakikawa, A., Bromage, TG., Cranfiled, MR., Stoinksi, TS., Schwartz, GT. In Press.. Molar wear in wild population of known-age mountain gorillas from Volcanoes National Park, Rwanda. Am J Phys Anthropol.

Godfrey, LR., Crowley, BE., Muldoon, KM., Kelley, EA., King, SJ., Best, AW., Berthaume, MA. 2015. What did *Hadropithecus* eat, and why should paleoanthropologists care. Am J Primatol 9999:1-15.

Godfrey, LR., Crowley, BE. Dumont, ER. 2011. Thinking outside the box: A lemur's take on hominin craniodental evolution. Proc Natl Acad Sci USA 108:E742.

Godfrey, LR., Jungers, WL., Reed, KE., Simons, EL. Chatrath, P. 1997. Primate subfossils: Inferences about past and present primate community structure. In: Goodman, S., Patterson, B., editors. Natural and Human Influenced Environmental Change in Madagascar. pp 218–256

Godfrey, LR., Jungers, WL. 2003. The extinct sloth lemurs of Madagascar. Evol Anthropol 12:252-263.

Godfrey, L. R., Rasoazanabary, E. 2012. Demise of the bet hedgers: A case study of human impacts on past and present lemurs of Madagascar. In: Sodikoff, G. M., editor. The Anthropology of Extinction: Essays on Culture and Species Death. pp 165–199.

Godfrey, L., Petto, AJ. Sutherland, MR. 2002. Dental ontogeny and life-history strategies: The case of the giant extinct Indroids of Madagascar. In: Plavcan, JM., Kay, RF., Jungers, WL., van Schaik, CP. Reconstructing Behavior in the Primate Fossil Record. New York: Kluwer Academic/Plenum. pp 113–157.

Godfrey, LR., Jungers, WL., Schwartz, GT. Irwin, MT. 2008. Ghosts and Orphans: Madagascar's Vanishing Ecosystems. Elwyn Simons: A Search for Origins. Chicagot: University of Chicago. pp 361–395.

Godfrey, LR, Samonds, KE, Jungers, WL, Sutherland, MR. 2003. Dental development primate life histories. in primate life histories and socioecology In: Kappeler, PM and Pereira, ME, editors. Chicago: University of Chicago, pp. 177–203.

Godfrey, LR., Samonds, KE., Jungers, WL., Sutherland, MR. Irwin, MT. 2004. Ontogenetic correlates of diet in Malagasy lemurs. Am J Phys Anthropol 123:250-276.

Godfrey, LR, Samonds , KE, Wright , PC, King, SJ. 2005. Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol (Basel). 76 2): 77–99.

Godfrey, LR., Semprebon, GM., Schwartz, GT., Burney, DA., Jungers, WL., Flanagan, EK. 2005. New insights into old lemurs: The trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825-854.

Godfrey, LR., Schwartz, GT., Samonds, KE., Jungers, WL. Catlett, KK. 2006. The secrets of lemur teeth. Evol Anthropol 15:142-154.

Godfrey, LR., Samonds, KE., Jungers, WL. Sutherland, MR. 2001. Teeth, brains, and primate life histories. Am J Phys Anthropol 114:192-214.

Godfrey, LR., Winchester, JM., King, J., Boyer, DM. Jernvall, J. 2012. Dental topography indicates ecological contraction of lemur communities. Am J Phys Anthropol 148:215-227.

Gonder, MK., Disotell, T. Oates, J. 2006. New genetic evidence on the evolution of chimpanzee populations and implications for taxonomy. Int J Primatol 27:1103-1127.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Cambridge: Harvard University Press.

Goodman, AH., Rose, JC. 1990. Assessment of systemic physiological perturbations from dental enamel hypoplasias and associated histological structures. Am J Phys Anthropol 33:59-110.

GRASS Development Team, 2014. Geographic Resources Analysis Support System (GRASS) Software v. 7.0. Open Source Geospatial Foundation Project. http://grass.osgeo.org

Grine, FE. 2005. Enamel thickness of deciduous and permanent molars in modern *Homo sapiens*. Am J Phys Anthropol 126:14-31.

Guatelli-Steinberg, D., Benderlioglu, Z. 2006. Brief communication: Linear enamel hypoplasia and the shift from irregular to regular provisioning in Cayo Santiago rhesus monkeys (*Macaca mulatta*). Am J Phys Anthropol 131:416-419.

Halliday, TJD., Goswami, A. 2013. Testing the inhibitory cascade model in Mesozoic and Cenozoic mammaliaforms. BMC Evol Biol 13:1-11.

Harcourt, AH., Fossey, D., Stewart, KJ. Watts, DP. 1980. Reproduction in wild gorillas and some comparisons with chimpanzees. J Reprod Fertil Suppl 28:59-70.

Hardin, AM, and Legge, SS. 2013. Geographic variation in nonmetric dental traits of the deciduous molars of *Pan* and *Gorilla*. Int J Primatol 34 (5): 1000–19.

Hawkes, K., O'Connell, JF., Jones, NGB., Alvarez, H. Charnov, EL.1998. Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci USA 95:1336-1339.

Hayssen, V. 1993. Empirical and theoretical constraints on the evolution of lactation. J Dairy Sci 76:3213-3233.

Hill, K., Barton, M. Hurtado, AM. 2009. The emergence of human uniqueness: Characters underlying behavioral modernity. Evol Anth 18:187-200.

Hill, K., Kaplan, H. 1999. Life history traits in humans: Theory and empirical studies. Ann Rev Anthropol 28:397-430.

Hillson, S. 2003. *Dental Anthropology*. Cambridge: Cambridge University Press.

Hillson, S. 2005. *Teeth*. Cambridge: Cambridge University Press.

Hogg, RT., Walker, RS. 2011. Life-history correlates of enamel microstructure in cebidae (Platyrrhini, Primates). Anat Rec 294:2193-2206.

Hogg, RT., Godfrey, LR., Schwartz, GT., Dirks, W. Bromage, TG. 2015. Lemur biorhythms and life history evolution. PLOS ONE 10:e0134210.

Howie, PW., Mcneilly, AS., Houston, MJ., Cook, A. Boyle, H. 1981. Effect of supplementary food on suckling patterns and ovarian activity during lactation. Brit Med J 283:757-759.

Hrdy, SB. 2009. Mothers and others: The evolutionary origins of mutual understanding. Harvard University Press: Belknap Press.

Humphrey, L., Dirks, W., Dean, C. Jeffries.2008. Tracking dietary transitions in weanling baboons (*Papio hamadryas anubis*) using strongtium/calcium ratios in enamel. Folia Primatol 79:197-212.

Humphrey, LT., Dean, CM., Jefferies, Teres E. Penn, M. 2008. Unlocking evidence of early diet from tooth enamel. Proc Natl Acad Sci, USA 105:6834-6839.

Humphrey, LT. 2010. Weaning behaviour in human evolution. Semin Cell Dev Biol 21:453-461.

Ingicco, T., Moigne, A.-M. Gommery, D. 2012. A deciduous and permanent dental wear stage system for assessing the age of *Trachypithecus* sp. specimens (Colobinae, Primates). J Arch Sci 39:421-427.

Irwin, MT. 2007. Ecologically Engimatic Lemurs: The sifakas of the Eastern forests (*Propithecus candidus, P. diadema, P. edwardsi, P. perrieri*, and *P. tattersalli*). In: Gould, L., Sauther, M. L., editors. Lemurs: Ecology and Adaptation. pp 305–326

Isler, K., van Schaik, CP. 2009. The expensive brain: A framework for explaining evolutionary changes in brain size. J Hum Evol 57:392-400.

Isler, K., van Schaik, CP. 2012. Allomaternal care, life history and brain size evolution in mammals J Hum Evol 63:52-63.

Jaeggi, AV., van, N., Maria A. van Schaik, CP. 2008. Begging for information: Mother offspring food sharing among wild Bornean orangutans. Am J Primatol 70:533-541.

Jaeggi, AV., Dunkel, LP., Noordwijk, MAV., Wich, SA., Sura, AAL, van Schaik, CP. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. Am J Primatol 72:62-71.

Janis, CM, Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol Rev Camb Philos Soc 63 (2): 197–230.

Janson, CH., van Schaik, CP. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira, ME., Fairbanks, LA., editors. Juvenile Primates: Life history, development, and behavior. Chicago: University of Chicago Press. pp 57–74.

Järvinen, E, Valimaki, K, Pummila, M, Thesleff, I, Jernvall, J. 2008. The taming of the shrew milk teeth. *Evol Dev* 10 (4): 477–86.

Jungers, WL., Demes, B. Godfrey, LR. 2008. How big were the "giant" extinct lemers of Madagascar? In: Fleagle, JG., Gilbert, CC., editors. Elwyn Simons: A Search for Origins. Chicago, IL: Unversity of Chicago. pp 343–360.

Kamilar, JM., Cooper, N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. Philos T R Soc B 368:1-10.

Kano, T. 1989. The sexual behavior of pygmy chimpanzees. In: Heltne, PG., Marquardt, L., eds. Understanding chimpanzees. Cambridge: Harvard University Press. p 176–183.

Kaplan, H., Hill, K., Lancaster, J. Hurtado, AM. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. Evol Anthropol 9:156-185.

Kappeler, PM., Fichtel, C. 2012. A 15-Year perspective on the social organization and life history of Sifaka in Kirindy Forest. In: Kappeler, PM., Watts, DP., editors. Long Term Field Studies of Primates. Springer Berlin Heidelberg. pp 101–121.

Kavanagh, KD, Evans, AR, Jernvall, J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449 (7161): 427–32.

Kawasaki, K., Tanaka, S. Ishikawa, T.. On the incremental lines in human dentine as revelaed by tetracycline labelling. J Anat 123:427-236.

Kay, RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol.43 (2): 195–216.

Kay, RF. 1981. The nut-crackers: A new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141-151.

Kelley, J., Schwartz, GT. 2010. Dental development and life history in living African and Asian apes. Proc Natl Acad Sci USA 107:1035-1040.

Kelley, J., Schwartz, GT. 2012. Life-history inference in the early hominins *Australopithecus* and *Paranthropus.* Int J Primatol 1-32.

Kennedy, GE. 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. J Hum Evol 48:123-145.

Keown, AJ., Bush, MB., Ford, C., Lee, JJW., Constantino, PJ. Lawn, BR. 2012. Fracture susceptibility of worn teeth. J Mech Behav Biomed 5:247-256.

Kiliaridis, S. 2006. The importance of masticatory muscle function in dentofacial growth. Seminars in Orthodontics 12:110-119.

King, SJ, Arrigo-Nelson, SJ, Pochron, ST, Semprebon, GM, Godfrey , LR, Wright, PC, Jernvall, J. 2005. Dental senescence in a long-lived primate links infant survival torainfall. Proc Natl Aca Sci, USA 102 (46): 16579–83.

King, SJ. 2004. Relative timing of ontogenetic events in primates. J Zool 264 (3): 267–80.

Kistler, L., Ratan, A., Godfrey, LR., Crowley, BE., Hughes, CE., Lei, R., Cui, Y., Wood, ML, Muldoon, KM, Andriamialison, H., McGraw, JJ, Tomsho, LP, Schuster, SC., Miller, W., Louis, EE, Yoder, AD, Malhi, RS., Perry, GH. 2015. Comparative and population mitogenomic analyses of Madagascar's extinct, giant subfossil lemurs. J Hum Evol 79:45-54.

Klukkert, ZS, Teaford, MF, Ungar, PS. 2012. A dental topographic analysis of chimpanzees. Am J Phys Anthropol .148 (2): 276-84.

Knott, CD, Kahlenberg, SM. 2011. Orangutans in perspective: understanding forced copulations. In Primates in Perspective, edited by C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, and R.M. Stumpf, 313–26. Oxford: Oxford University Press.

Kuroda, S. 1989. Developmental retardation and behavioral characteristics of pygmy chimpanzees. In: Heltne, P. G., Marquardt, L., editors. Understanding chimpanzees. Cambridge: Harvard University Press. pp 184–193.

Kupczik, K., Lev-Tov, N. 2014. The adaptive significance of enamel loss in the mandibular incisors of cercopithecine primates (Mammalia: Cercopithecidae): A finite element modeling study. PLOS ONE 9:e97677.

Kutner, MH., Nachtsheim, CJ., Neter, J. Li, W. 2005. Applied linear statistical models. 5 edition. Boston: McGraw Hill.

Kuzawa, CW., Bragg, JM. 2012. Plasticity in human life history strategy implications for contemporary human variation and the evolution of genus *Homo.* Curr Anthropol 53:S369-S382.

Lambert, JE., Rothman, JM. 2015. Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. Annu Rev Anthropol 44:493-512.

Langer, P. 2008. The phases of maternal investment of eutherian mammals. Zoology 111:148-162.

Lathouwers, MD., Elsacker, LV. 2006. Comparing infant and juvenile behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): A preliminary study. Primates 47:287-293.

Le Gros Clark, WE. 1947. Observations on the anatomy of the fossil australopithecinae. J Anat 83:300-333.

Lee, PC. 1996. The meanings of weaning: growth, lactation, and life history. Evol Anth 5:87-98.

Lee, JJW., Constantino, PJ., Lucas, PW. Lawn, BR. 2011. Fracture in teeth-a diagnostic for inferring bite force and tooth function. Biol Rev 86:959-974.

Leigh, SR., Shea, BT. 1996. Ontogeny of body size variation in african apes. Am J Phys Anthropol 99:43-65.

Leigh, SR. 1994. Ontogenetic correlates of diet in anthropoid primates. Am J Phys Anthropol 94:499-522.

Lucas, PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: CambridgeUniversity Press.

Lucas, PW, Corlett, RT, Luke, DA. 1986. Postcanine tooth size and diet in anthropoid primates. Zeitschrift fur Morphologies und Anthropologie 253–76.

Lucas, PW., Casteren, AV., Al-Fadhalah, K., Almusallam, AS., Henry, AG., Michael, S. 2014. The role of dust, grit and phytoliths in tooth wear. Annales Zoologici Fennici Annales Zoologici Fennici 51:143-152.

Lucas, PW, Omar, R, Al-Fadhalah, K., Almusalla, AS, Henry, AG, Michael, S. Thai, LA, Watzke, J., Strait, DS, Atkins, AG. 2013. Mechanisms and causes of wear in tooth enamel: Implications for hominin diets. Journal of The Royal Society Interface 10:1-9.

Macena, MCB., Tornisiello Katz, CR., Heimer, MV., De Oliveira E Silva, JF. Costa, LB. 2011. Space changes after premature loss of deciduous molars among Brazilian children. Am J Orthod Dentofac 140:771-778.

Macchiarelli, R., Bondioli, L., Debenath, A., Mazurier, A., Tournepiche, JF., Birch, W. Dean, MC.2006. How Neanderthal molar teeth grew. Nature 444:748-751.

Macho, GA. 2001. Primate molar crown formation times and life history evolution revisited. Am J Primatol 55:189-201.

Macho, GA., Spears, IR. 1999. Effects of loading on the biochemical behavior of molars of *Homo*, *Pan*, and *Pongo.* Am J Phys Anthropol 109:211-227.

Macho, GA., Lee-Thorp, JA. 2014. Niche partitioning in sympatric *Gorilla* and *Pan* from Cameroon: implications for life history strategies and for reconstructing the evolution of hominin life history. Plos One 9:e102794.

Maclean, EL., Barrickman, N.L., Johnson, E.M. Wall, CE. 2009. Sociality, ecology, and relative brain size in lemurs. J Hum Evol 56:471- 478.

Mahoney, P. 2011. Human deciduous mandibular molar incremental enamel development. Am J Phys Anthropol 144:204-214.

Mahoney, P. 2013. Testing functional and morphological interpretations of enamel thickness along the deciduous tooth row in human children. Am J Phys Anthropol 151(4):518-25.

Mahoney, P. 2015. Dental fast track: Prenatal enamel growth, incisor eruption, and weaning in human infants. Am J Phys Anthropol 156:407-421.

Mandalaywala, TM., Higham, JP., Heistermann, M., Parker, KJ. Maestripieri, D. 2014. Physiological and behavioural responses to weaning conflict in free-ranging primate infants. Animal Behaviour 97:241-247.

Mann, A. 1975. Paleodemographic aspects of the South African australopithecines. University of Pennsylvania, Philadelphia, USA.

Martin, RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293:57-60.

Martin, RD.1990. Primate Origins and Evolution: A Phylogenetic Reconstruction. Chapman and Hall.

Martin, R.D. 2007. The evolution of human reproduction: A primatological perspective. Yrbk Phys Anthropol 134:59-84.

Martin, RD., Maclarnon, AM. 1985. Gestation period, neonatal size and maternal investment in placental mammals. Nature 313:220-223.

Matthew, MS., Zeresenay, A., Charleen, G. Jean-Jacques, H. 2015. Enamel thickness trends in Plio-Pleistocene hominin mandibular molars. J Hum Evol 85:35-45.

Marshall, AJ., Boyko, CM., Feilen, KL., Boyko, RH. Leighton, M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. Am J Phys Anthropol 140:603-614.

Matsuda, I., Tuuga, A., Hashimoto, C., Bernard, H., Yamagiwa, J., Fritz, J., Tsubokawa, K., Yayota, M., Murai, T., Iwata, Y., Clauss. 2014. Faecal particle size in free-ranging primates supports a 'rumination' strategy in the proboscis monkey (*Nasalis larvatus*). Oecologia 174:1127-1134.

Marshall, AJ., Wrangham, RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219-1235.

McLeod, AI. 2011. Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2. https://CRAN.R-project.org/package=Kendall

McNeilly, AS., Tay, CCK. Glasier, A. 1994. Physiological mechanisms underlying lactational amenorrhea. Annals of the New York Academy of Sciences 709:145-155.

Metcalf, CJE., Pavard, S. 2007. Why evolutionary biologists should be demographers? Trends Ecol Evol 22:205-212.

M'Kirera, F.,Ungar, P. S. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla.* Am J Primatol 60:31-41.

Millette, JB., Sauther, ML., Cuozzo, FP. Ness, JL. 2012. The impact of dental impairment on ring-tailed lemur food processing performance. Am J Phys Anthropol 148:238-248.

Mittermeier, RA., Ganzhorn, JU., Konstant, WR., Glander, K., Tattersall, I., Groves, CP.,Rylands, AB, Hapke, A., Ratsimbazafy, J., Mayor, MI., Louis Jr., EE., Rumpler, Y.,Schwitzer, C. Rasoloarison, RM. 2008. Lemur diversity in Madagascar. Int J Primatol 29:1607-1656.

Molnar, S., Gantt, DG. 1977. Functional implications of primate enamel thickness. Am J Phys Anthropol 46:447-454.

Molnar, S., Przybeck, TR., Gantt, DG., Elizondo, RS. Wilkerson, JE. 1981. Dentin apposition rates as markers of primate growth. Am J Phys Anthropol 55:443-453.

Moimaz, SAS., Araújo, PC., Chiba, FY., Garbín, CA.S. Saliba, NA. 2013. Prevalence of deciduous tooth erosion in childhood. Int J Dent Hygiene 11:226-230.

Muggeo, VM. 2003. Estimating regression models with unknown break-points. Statistics in Medicine 15:3055-3071.

Muggeo, VMR. 2008. Segmented: an R Package to fit regression models with broken-line relationships. R News, 8/1, 20-25. URL http://cran.r-project.org/doc/Rnews/.

Nanci, A. 2013. Ten Cate's Oral Histology: Development, Structure, and Function (8 ed.). St. Louis: Elsevier Mosby.

Navarrete, A., van Schaik, CP. Isler, K. 2011. Energetics and the evolution of human brain size. Nature 480:91-93.

Norconk, MA., Wright, BW., Conklin-Brittain, NL. Vinyard, C. J. 2009. Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garger, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. W. Strier, K. B. eds. South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation. Springer. pp 279–319.

Nowell, AA., Fletcher, AW. 2007. Development of independence from the mother in *Gorilla gorilla gorilla.* Int J Primatol 28:441-455.

Ohba, M., Samonds, KE., Lafleur, M., Ali, JR. Godfrey, LR. 2016. Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. Palaeogeogr Palaeocl 441:688-695.

Olofsson, H., Ripa, J. Jonzen, N. 2009. Bet-hedging as an evolutionary game: The trade-off between egg size and number. P R Soc B 276:2963-2969.

Orlando, L., Calvignac, S., Schnebelen, C., Douday, CJ., Godfrey, LR. Hänni, C. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evol Biol 8:1-9.

Perez, VR., Godfrey, LR., Nowak-Kemp, M., Burney, DA., Ratsimbazafy, J. Vasey, N. 2005. Evidence of early butchery of giant lemurs in Madagascar. J Hum Evol 49:722-742.

Osborn, HF. 1907. Evolution of Mammalian Molar Teeth: To and From the Triangular Type Including Collected and Revised Researches Tritubercuły and New Sections on the Forms. (Biological Studies and Addresses. Vol. I). London: MacMillan.

Owen, R. 1840. Odontography; Or, a Treatise on the Comparative Anatomy of the Teeth; Their Physiological Relations, Mode of Development, and Microscopic Structure, in the Vertebrate Animals. By Richard Owen. Longon: Hippolyte Baillière.

Plavcan, JM. 2001. Sexual dimorphism in primate evolution. Yrbk Phys Anthropol 44:25-53.

Plavcan, JM. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: Implications for the fossil record. Am J Phys Anthropol 120:38-60.

Polk, JD., Williams, SA., Peterson, JV., Roseman, C. Godfrey, LR. 2010. Subchondral bone apparent density and locomotor behavior in extant primates and subossil lemurs *Hadropithecus* and *Pachylemur.* Int J Primatol 31:275-299.

Polly, PD. 2007. Evolutionary biology: Development with a bite. Nature 449:413-415.

Pontzer, H., Raichlen, DA., Gordon, AD., Schroepfer-Walker, KK., Hare, BO, Äôneill, MC., Muldoon, KM, Dunsworth, H., Wood, BM., Isler, K.,Burkart, J., Irwin, M., Shumaker, RW, Lonsdor, EV, Ross, SR. 2014. Primate energy expenditure and life history. Proc Natl Acad Sci USA111:1433-1437.

Poux, C., Madsen, O., Marquard, E., Vieites, DR., De Jong, WW. Vences, M. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Systematic Biology 54:730-719.

Prinz, JF., Lucas, PW. 1995. Swallow thresholds in human mastication. Arch of Oral Biol 40:401-403.

Pusey, AEE. 1983. Mother offspring relationships in chimpanzees after weaning. Anim Behav 31:363-377.

RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rabenold, D, Pearson, OM. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. PLoS ONE 6 (12): e28379.

Ramirez-Rozzi, F., Lacruz, R. 2007. Histological study of an upper incisor and molar of a bonobo (*Pan paniscus*) individual. In: Bailey, SE, Hublin, JJ., editors. Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Dordrecht, the Netherlands: Springer. Pp. 163–176.

Reed, KE and Fish, JL. 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, DK and van Schaik , CP. Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates. Cambridge: Cambridge University Press, p. 489-518.

Reid, DJ., Schwartz, GT., Dean, C. Chandrasekera, MS. 1998. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J Hum Evol 35:427-448.

Reid, DJ., Ferrell, RJ. 2006. The relationship between number of striae of Retzius and their periodicity in imbricational enamel formation. J Hum Evol 50:195-202.

Reitsema, LJ. 2012. Introducing fecal stable isotope analysis in primate weaning studies. Am J Primatol 74:926-939.

Renvoisé, E., Evans, AR., Jebrane, A., Labruère, C., Laffont, R. Montuire, S. 2009. Evolution of mammal tooth patterns: New insights from a developmental prediction model. Evolution 63:1340-1327.

Richard, AF., Dewar, RE., Schwartz, M. Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). J Zool 256:421-436.

Robson, SL., Wood, B. 2008. Hominin life history: Reconstruction and evolution. J Anat 212:394-425.

Robson, SL., van Schaik, CP. Hawkes, K. 2006. The derived features of human life history. In: Hawkes, K., Paine, R. R., editors. The evolution of human live history. Santa Fe: School of American Research Press. pp 17–44.

Roff, DA. 2002. Life history evolution. Sunderland, Massachusetts: Sinauer Associates, Inc.

Rosenberger, AL, Kinzey, WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45 (2): 281–97.

Rubenstein, DR. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proc Natl Acad, USA 108:10816-10822.

Rumpler, Y., Hauwy, M., Fausser, JL., Roos, C., Zaramody, A., Andriaholinirina, N, Zinner, D. 2011. Comparing chromosomal and mitochondrial phylogenies of the Indriidae (Primates, Lemuriformes). Chromosome Res 19:209-224.

Russon, AE. 2006. Acquisition of complex foraging skills in juvenile and adolescent orangutans (*Pongo pygmaeus*): Developmental influences. Aquatic Mammals 32:500-510.

Russon, AE., van Schaik, CP., Kuncoro, P., Ferisa, A., Hadayani, DP. van Noordwijk, MA. 2009. Innovation and intelligence in orangutans. In: Wich, SA., Utami, SS., Mitra Setia, T. van Schaik, C. editors. Orangutans: Geographic Variation in Behavioral Ecology and Conservation. Oxford: Oxford University Press. pp 279–298.

Russon, AE., Compost, A., Kuncoro, P. Ferisa, A. 2014. Orangutan fish eating, primate aquatic fauna eating, and their implications for the origins of ancestral hominin fish eating. J Hum Evol 50-63.

Sacher, GA. 1959. Relation of lifespan to brain weight and body weight in mammals. London: Churchill.

Sanson, GD., Kerr, SA. Gross, KA. 2007. Do silica phytoliths really wear mammalian teeth? Am J Phys Anthropol 34:526-531.

Sardi, M. L., Ramirez-Rozzi, F. 2007. Developmental connections between cranial components and the emergence of the first permanent molar in humans. J Anat 210:406-417.

Scott, RS., Teaford, MF. Ungar, PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Schoeninger, MJ. 2014. Stable isotope analyses and the evolution of human diets. Annu Rev Anthropol 43:413-430.

Segura, AM., Milessi, AC., Vögler, R., Galván-Magaña, F. Muggeo, V. 2013. The determination of maturity stages in male elasmobranchs (Chondrichthyes) using a segmented regression of clasper length on total length. Can J Fish Aquat Sci 70:830-833.

Schroer, K., Wood, B. 2015. Modeling the dental development of fossil hominins through the inhibitory cascade. J Anat 226:150-162.

Schultz, AH. 1956. Postembryonic age changes. Primatologia 1:887-964.

Schwartz, GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. Am J Phys Anthropol 111:221 244.

Schwartz, GT. 2012. Growth, development, and life history throughout the evolution of *Homo.* Curr Anthropol 53:S395-S408.

Schwartz, GT., Dean, MC. 2008. Charting the chronology of developing dentitions. In: Irish, JD., Nelson, GC., editors. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press. pp 219–233.

Schwartz, GT., Mahoney, P., Godfrey, LR., Cuozzo, FP., Jungers, WL. Randria, GFN. 2005. Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): Implications for understanding life history variation in subfossil lemurs. J Hum Evol 49:702-721.

Schwartz, GT, Samonds, KE, Godfrey, LR, Jungers, WL, Simons, EL. 2002. Dental microstructure and life history in subfossil Malagasy lemurs. Pro Natl Acad Sci, USA 99 (9): 6124–29.

Schwitzer, C., Mittermeier, RA., Johnson, SE., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, Raxafindramanana, J., Louis Jr, EE, Chikhi, L., Colquhon, IC, Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., Wright, PC. 2014. Averting lemur extinctions amid Madagascar's political crisis. Science 343:842-843.

Scott, JE. 2012. Molar size and diet in the strepsirrhini: Implications for size-adjustment in studies of primate dental adaptation. J Hum Evol 63:796-804.

Scott, JR., Godfrey, LR., Jungers, WL., Scott, RS., Simons, EL., Teaford, MF, Ungar, PS, Walker, A. 2009. Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. J Hum Evol 56:405-416.

Scott, RS., Teaford, MF. Ungar, PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Sellen, DW. 2001. Comparison of infant feeding patterns reported for nonindustralised populations with current recommendations. J Nutr 131:2707-2715.

Shellis, RP., Beynon, AD., Reid, DJ. Hiiemae, KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507-522.

Sibly, RM., Brown, JH. 2007. Effects of body size and lifestyle on evolution of mammal life histories. Proc Natl Acad Sci USA 104:17707-17712.

Simpson, GG. 1936. Studies on the earliest mammalian dentition. Dental Cosmos 78: 791–800.

Skinner, M. 1997. Dental wear in immature late Pleistocene European hominines. J Arch Sci 24:677-700.

Smith, BH. 1989. Dental development as a measure of life history in primates. Evolution 43:683-688.

Smith, BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:134-142.
Smith, BH., Boesch, C. 2011. Mortality and the magnitude of the "wild effect" in chimpanzee tooth emergence. J Hum Evol 60:34-46.

Smith, BH, Crummett, TL Brandt, KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yrbk Phys Anthropol 37 177–231.

Smith, BH., Tompkins, RL. 1995. Toward a life-history of the hominidae. Ann Rev Anthropol 24:257-279.

Smith, CC., Morgan, ME. Pilbeam, D.2010. Isotopic ecology and dietary profiles of Liberian chimpanzees. J Hum Evol 58:43 - 55.

Smith, RJ., Gannon, PJ. Smith, BH. 1995. Ontogeny of australopithecines and early *Homo* - evidence from cranial capacity and dental eruption. J Hum Evol 29:155-168.

Smith, TM. 2006. Experimental determination of the periodicity of incremental features in the enamel. J Anat 208:125-138.

Smith, TM., Reid, DJ. Sirianni, JE. 2006. The accuracy of histological assessments of dental development and age at death. J Anat 208:125-138.

Smith, TM., Tafforeau, P., Reid, DJ., Grun, R., Eggins, S., Boutakiout, M. Hublin, J-J. 2007. Earliest evidence of modern human life history in north african early homo sapiens. Proc Natl Acad Sci USA 104:6128-6133.

Smith, TM. 2013. Teeth and human life-history evolution. Annu Rev Anthropol 42:191-208.

Smith, TM., Kupczik, K., Machanda, Z., Skinner, M. M. Zermeno, J. P. 2012. Enamel thickness in Bornean and Sumatran orangutan dentitions. Am J Phys Anthropol 147:417-426.

Smith, TM., Machanda, Z., Bernard, AB., Donovan, RM., Papakyrikos, AM., Muller, MN, Wrangham, R. W. 2013. First molar eruption, weaning, and life history in living wild chimpanzees. Proc Natl Acad Sci 110:2787-2791.

Smith, TM., Tafforeau, P., Reid, D. J., Grun, R., Eggins, S., Boutakiout, M. 2007. From the cover: Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci USA 104:6128-6133.

Sokal, RR., Rohlf, JF. 1994. Biometry: The Principles and Practices of Statistics in Biological Research. 3rd ed. New York: WH. Freeman and Co.

Sponheimer, M., Alemseged, Z., Cerling, T. E., Grine, F. E., Kimbel, W. H., Leakey, M. G. Lee-Thorp, JA, Manth, FK, Reed, KE, Wood, BA, Wynn, JG. 2013. Isotopic evidence of early hominin diets. Proc Natl Acad Sci, USA 110:10513-10518.

Stearns, SC. 1992. The evolution of life histories. New York: Oxford.

Sterling, EJ. 1994. Evidence for nonseasonal reproduction in wild aye-aye (*Daubentonia madagascariensis*). Folia Primatol (Basel) 62:46-53.

Stewart, KJ. 1988. Suckling and lactational anestrus in wild gorilla (*Gorilla gorilla*). J Reprod Fertil 83:627-634.

Stoinski, TS., Perdue, B., Breuer, T. Hoff, MP. 2013. Variability in the developmental life history of the genus *Gorilla.* Am J Phys Anthropol 1-8.

Stroik, L. 2014. The dietary competitive environment of the origination and early diversification of Euprimates in North America. PhD Dissertation. Arizona State University.

Stumpf, R. 2011. Chimpanzees and bonobos: Inter- and Intraspecies Diversity. In: Campbell, C.J., Fuentes, A., Mackinnon, KC., Bearder, SK. Stumpf, RM. editors. Primates in Perspective. Oxford: Oxford University Press. pp 340–356.

Swindler, DR. 2002. Primate dentition: An introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

Tanaka, E. M., Sato, S. 2008. Longitudinal alteration of the occlusal plane and development of different dentoskeletal frames during growth. Am J Orthod Dentofac 134:602.e1-602.e11.

Teaford, M. F. 1988. A review of dental microwear and diet in modern mammals. Scanning Microsc 2:1149-1166.

Teaford, M. F. 2000. Primate dental functional morphology revisited. Development, function and evolution of teeth Cambridge: Cambridge University Press p 290-304.

Teaford, M. F., Ungar, P. S. 2000. Diet and the evolution of the earliest human ancestors. Pro Natl Acad Sci USA 97:13506-13511.

Thompson, ME. 2013. Comparative Reproductive Energetics of Human and Nonhuman Primates. In: Brenneis, D., Strier, KB., editors. 42. pp 287–304

Thompson, ME., Müller, MN. Wrangham, RW. 2012. The energetics of lactation and the return to fecundity in wild chimpanzees. Behav Ecology 23:1234-1241.

Trivers, R. L. 1974. Parent-offspring conflict. Am Zool 14:249-264.

Trotter, M., Hixon, BB. Macdonald, BJ. 1977. Development and size of the teeth of *Macaca mulatta.* Am J Anat 150:109-127.

Tutin, CEG., McGinnis, PR. 1981. Chimpanzee reproduction in the wild. In: Graham, C. E., ed. Reproductive biology for the great apes: Comparative and biomedical perspectives. New York: Academic Press. p 239–264.

Ungar, PS. 2007. Dental topography and human evolution. In: Bailey, SE., Hublin, JJ., editors. Dental perspectives on human evolution: state of the art research in dental paleoanthropology. Dordrechet: Springer. p 321–344.

Ungar, PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46 (5): 605–22.

Ungar, PS. 2010. Mammal teeth: origin, evolution, and diversity. Baltimore: The John Hopkins University Press.

Ungar, PS, M'Kirera, F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proc Natl Acad Sci, USA* 100 (7): 3874–77.

Ungar, PS, Williamson, M. 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. http://palaeo-electronica.org/2000_1/gorilla/issue1_00.htm.1(18):
1–18.

van Noordwijk, MA., van Schaik, CP. 2005. Development of ecological competence in Sumatran orangutans. Am J Phys Anthropol 127:79-94.

van Noordwijk., Kuzawa , MA., van Schaik, CP. 2013. The evolution of the patterning of human lactation: a comparative perspective. Evol Anthropol 22:202-212.

van Noordwijk, M. A, Willems, E. P., Atmoko, S. S. U., Kuzawa, C. W. van, S., Carel P. 2013. Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). Behav ecol sociobiol 67:805-814.

van Noordwijk, MA., Sauren, SEB., Nuzuar, AA., Morrogh-Bernard, HC., Utami Atmoko, SS. van Schaik, CP. 2009. Development of independence. In: Wich, SA., Utami, SS., Mitra Setia, T. van Schaik, C. editors. Orangutans: Geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 189–204.

Veiberg, V, Mysterud, A., Bjorkvoll, E., R Langvatn, LE., Loe, Irvine, RJ, Bonenfant, C., Couweleers, F., and Stenseth, NC. 2007. Evidence for a trade-off between early growth and tooth wear in Svalbard reindeer. J Anim Ecol 76 (6): 1139–48.
Venkataraman, VV, Glowacka, H, Fritz, J, Clauss, M, Seyoum, C, Nguyen, N, Fashing, PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155 (1): 17–32.

Vitzthum, V. J. 1994. Comparative study of breastfeeding structure and its relation to human reproductive ecology. Yrb Phys Anthropol 37:307-349.

Vogel, ER., van, W., JT, Lucas, PW., Atmoko, SSU., van, S., CP, Dominy, NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii.* J Hum Evol 55:60-74.

Walker, A., Hoeck, HN. Perez, L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201:908-910.

Warton, DI., Duursma, RA., Falster, DS. Taskinen, S. 2012. Smatr 3 - An R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3:257-259.

Watts, DP. 1991. Mountain gorilla reproduction and sexual behavior. Am J Primatol 24:211-225.

Wheatley, D., Gillings, M. 2002. Spatial technology and archaeology: The archaeological applications of GIS. Boca Raton: Taylor and Francis.

Weisbecker, V., Goswami, A. 2010. Brain size, life history, and metabolism at the marsupial/placental dichotomy. Proc Natl Acad Sci, USA 107:16216-16221.

Wich, SA., Utami-Atmoko, SS., Setia, TM., Rijksen, HD., Schurmann, C., van Hooff, JA. 2004. Life history of wild sumatran orangutans (*Pongo abelii*). J Hum Evol 47:385-398.

Wickham, H. 2009. Ggplot2: elegant graphics for data analysis. New York: Springer.

Williams, GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:411-398.

Wilson, LB., Sánches-Villagra, MR., Madden, RH. Kay, RF, 2012. Testing a developmental model in the fossil record: Molar proportions in South American ungulates. Paleobiology 38:308-321.

Winchester, JM., Boyer, DM., St. Clair, EM., Gosselin-Ildari, AD., Cooke, SB. Ledogar, JA. 2014. Dental topography of platyrrhines and prosimians: Convergence and contrasts. Am J Phys Anthropol 153:29-44.

Won, YJ., Hey, J. 2005. Divergence population genetics of chimpanzees. Mol Biol Evol 22:297-307.

Wood, B., Schroer, K. 2012. Reconstructing the diet of an extinct hominin taxon: Therole of extant primate models. Int J Primatol 33:716-742.

Wright, PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Am J Phys Anthropol Suppl 29:31-72.

Wright, PC., Razafindratsita, VR., Pochron, ST. Jernvall, J. 2005. The Key to Madagascar Frugivores. In: Dew, JL., Boubli, JP., editors. Tropical Fruits and Frugivores: The Search for Strong Interactors. pp 121–138.

Yamagiwa, J., Basabose, A. K. 2009. Fallback foods and dietary partitioning among *Pan* and *Gorilla.* Am J Phys Anthropol 140:739-750.

Yamashita, N., Cuozzo, FP. Sauther, ML. 2012. Interpreting food processing through dietary mechanical properties: A lemur catta case study. Am J Phys Anthropol 148:205 214.

Zehr, SM., Roach, RG., Haring, D., Taylor, J., Cameron, FH. Yoder, AD. 2014. Life history profiles for 27 strepsirrhine primate taxa generated using captive data from the duke lemur center. Sci Data 1:140019.

Zihlman, A., Bolter, D. Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. Proc Natl Acad Sci USA 101:10541-10543.

Zuccotti, LF, MD Williamson, WF Limp, and PS Ungar. 1998. Technical note:modeling primate occlusal topography using geographic information systems technology. Am J Phys Anthropol 107 (1): 137–42.

APPENDIX A

SPECIMEN INFORMATION AND DATA MEASUREMENTS

Abbreviations

AMNH - American Museum of Natural History, New York

CMNH - Natural History Museum, Cleveland

KBINS – Natural History Museum, Brussels

MCZ - Museum of Comparative Zoology, Cambridge

RMCA - Royal Museum of Central Africa, Tervuren

PC - Powell-Cotton Museum, Birchington-by-the-Sea

USNM - National Museum of Natural History, Washington D.C.

ZSM - Zoological State Museum, Munich

Zurich - University of Anthropology, Zurich

Museum	Individual	Status	Dental Score	Species	Slope (Mean)	Angularity (Mean)	RFI	OPCR	PDE	Weaning Status
RMCA	RMCA 5484	wild	0.620	*Gorilla beringei beringei*	43.14	87.86	170.08	52.13	0.97	Weaned
USNM	USNM 239884	wild	0.582	*Gorilla beringei beringei*	46.49	87.86	170.05	51.50	0.00	Not Weaned
USNM	USNM 241232	wild	0.788	*Gorilla beringei beringei*	41.48	87.52	165.97	53.63	8.17	Weaned
KBINS	KBIN 6870	wild	0.519	*Gorilla beringei graueri*	45.39	87.62	171.07	56.50	0.00	Not Weaned
RMCA	RMCA 808	wild	0.615	*Gorilla beringei graueri*	43.79	87.72	164.85	58.75	0.52	Weaned
RMCA	RMCA 29318	wild	0.697	*Gorilla beringei graueri*	35.67	86.72	152.10	63.00	21.12	Weaned
KBINS	KBINS 1583F	wild	0.596	*Gorilla beringei graueri*	46.08	87.29	170.93	58.75	0.00	Not Weaned
RMCA	RMCA 11726	wild	0.760	*Gorilla beringei graueri*	35.36	86.36	142.25	62.00	11.75	Weaned
RMCA	RMCA 15358	wild	0.587	*Gorilla beringei graueri*	49.19	87.54	191.03	58.75	0.00	Not Weaned
RMCA	RMCA 14616	wild	0.591	*Gorilla beringei graueri*	49.76	87.86	194.16	58.13	0.00	Not Weaned
RMCA	RMCA 14305	wild	0.591	*Gorilla beringei graueri*	43.27	87.67	167.44	53.13	1.01	Not Weaned

RMCA	RMCA 811	wild	0.846	*Gorilla beringei graueri*	33.97	86.82	141.73	65.25	15.59	Weaned
RMCA	RMCA 810	wild	0.663	*Gorilla beringei graueri*	37.41	87.38	155.29	62.00	9.20	Weaned
RMCA	RMCA 996	wild	0.615	*Gorilla beringei graueri*	42.52	87.68	165.97	55.50	5.87	Weaned
MCZ	MCZ 231817	wild	0.615	*Gorilla beringei graueri*	41.96	87.82	160.54	51.88	1.43	Weaned
RMCA	RMCA 12284	wild	0.543	*Gorilla beringei graueri*	46.26	88.11	189.55	59.38	0.00	Not Weaned
RMCA	RMCA 11724	wild	0.615	*Gorilla beringei graueri*	46.35	87.95	179.53	59.50	0.12	Weaned
RMCA	RMCA 12285	wild	0.587	*Gorilla beringei graueri*	44.09	87.83	172.61	55.63	1.38	Not Weaned
CMNH	HTB 2768	wild	0.596	*Gorilla gorilla gorilla*	37.29	86.75	151.16	51.75	0.00	Not Weaned
PC	PC CAM II 3	wild	0.572	*Gorilla gorilla gorilla*	42.61	87.54	164.76	50.25	0.52	Not Weaned
PC	PC FC 147	wild	0.745	*Gorilla gorilla gorilla*	30.03	85.66	132.43	41.63	14.20	Not Weaned
PC	PC FC 151	wild	0.750	*Gorilla gorilla gorilla*	33.11	86.52	137.71	61.00	16.43	Not Weaned
PC	PC M000 Ser2	wild	0.635	*Gorilla gorilla gorilla*	40.69	87.29	156.53	61.63	6.17	Not Weaned

PC	PC M000 Ser1	wild	0.625	*Gorilla gorilla gorilla*	40.49	86.59	154.12	45.25	0.82	Not Weaned
PC	PC M117	wild	0.587	*Gorilla gorilla gorilla*	42.35	87.54	160.32	49.50	0.10	Not Weaned
PC	PC M119 Ser	wild	0.678	*Gorilla gorilla gorilla*	36.69	87.16	148.07	60.13	10.45	Not Weaned
PC	PC M137	wild	0.582	*Gorilla gorilla gorilla*	42.49	87.41	163.68	49.50	0.03	Not Weaned
PC	PC M160	wild	0.817	*Gorilla gorilla gorilla*	38.89	87.02	153.53	58.88	10.64	Not Weaned
PC	PC M169 Ser	wild	0.635	*Gorilla gorilla gorilla*	37.23	87.59	148.92	47.00	1.46	Not Weaned
PC	PC M29	wild	0.596	*Gorilla gorilla gorilla*	45.03	87.25	168.36	54.25	0.54	Not Weaned
PC	PC M319	wild	0.798	*Gorilla gorilla gorilla*	37.64	87.17	152.59	57.25	8.24	Not Weaned
PC	PC M33	wild	0.678	*Gorilla gorilla gorilla*	35.69	86.79	145.44	54.50	5.83	Not Weaned
PC	PC M333	wild	0.606	*Gorilla gorilla gorilla*	42.70	87.27	160.70	53.25	0.23	Not Weaned
PC	PC M409	wild	0.596	*Gorilla gorilla gorilla*	40.21	87.05	157.55	47.13	2.74	Not Weaned
PC	PC M450	wild	0.635	*Gorilla gorilla gorilla*	34.89	86.16	147.54	53.38	9.40	Not Weaned
PC	PC M471	wild	0.596	*Gorilla gorilla*	41.92	87.47	157.91	51.25	0.00	Not Weaned

				gorilla						
PC	PC M487	wild	0.625	*Gorilla gorilla gorilla*	38.15	87.04	157.68	57.00	3.46	Not Weaned
PC	PC M497	wild	0.582	*Gorilla gorilla gorilla*	42.57	87.65	167.15	56.38	0.00	Not Weaned
PC	PC M698	wild	0.654	*Gorilla gorilla gorilla*	35.38	86.15	145.38	58.13	8.04	Not Weaned
PC	PC M760	wild	0.649	*Gorilla gorilla gorilla*	40.06	87.09	159.07	53.25	0.87	Not Weaned
PC	PC M847	wild	0.731	*Gorilla gorilla gorilla*	34.70	85.26	143.47	56.63	9.98	Not Weaned
PC	PC M855	wild	0.649	*Gorilla gorilla gorilla*	38.04	87.25	154.11	62.25	6.66	Not Weaned
PC	PC M865	wild	0.769	*Gorilla gorilla gorilla*	34.81	86.95	146.18	68.00	20.80	Weaned
PC	PC M32 Series1	wild	0.846	*Gorilla gorilla gorilla*	39.20	87.17	169.16	54.88	14.14	Weaned
PC	PC M32 Seriies2	wild	0.582	*Gorilla gorilla gorilla*	45.88	87.49	169.63	51.00	13.13	Not Weaned
AMNH	AMNH 114217	wild	0.558	*Gorilla gorilla gorilla*	38.99	87.49	151.91	66.63	1.43	Not Weaned
CMNH	HTB 2772	wild	0.611	*Gorilla gorilla gorilla*	37.37	87.10	155.20	54.25	8.34	Not Weaned
CMNH	HTB 1753	wild	0.716	*Gorilla gorilla gorilla*	29.15	86.07	130.39	54.13	8.20	Weaned

CMNH	HTB 2754	wild	0.596	*Gorilla gorilla gorilla*	40.69	87.56	155.23	54.50	1.02	Not Weaned
CMNH	HTB 3554	wild	0.596	*Gorilla gorilla gorilla*	39.19	87.31	149.47	50.88	5.53	Not Weaned
CMNH	HTB 1760	wild	0.615	*Gorilla gorilla gorilla*	34.39	87.08	137.18	48.13	3.41	Not Weaned
CMNH	HTB 1799	wild	0.558	*Gorilla gorilla gorilla*	39.89	87.80	159.14	50.25	0.00	Not Weaned
CMNH	HTB 1943	wild	0.654	*Gorilla gorilla gorilla*	37.69	86.07	150.16	56.25	6.29	Not Weaned
CMNH	HTB 1949	wild	0.952	*Gorilla gorilla gorilla*	30.48	85.38	142.78	50.88	40.75	Weaned
ZSM	ZSM 1913 1163	wild	0.606	*Gorilla gorilla gorilla*	38.89	86.98	152.36	53.88	1.08	Not Weaned
Zurich	ZURICH 1250	wild	0.606	*Gorilla gorilla gorilla*	41.43	87.37	159.27	53.88	0.67	Not Weaned
Zurich	ZURICH 6610	wild	0.625	*Gorilla gorilla gorilla*	39.98	87.74	159.99	58.50	0.72	Not Weaned
Zurich	ZURICH 6681	wild	0.567	*Gorilla gorilla gorilla*	44.53	87.77	163.97	56.00	0.12	Not Weaned
Zurich	ZURICH 6782	wild	0.615	*Gorilla gorilla gorilla*	48.37	87.97	177.42	61.50	0.49	Not Weaned
Zurich	ZURICH 6844	wild	0.558	*Gorilla gorilla gorilla*	44.68	87.71	164.77	59.13	0.00	Not Weaned
Zurich	ZURICH	wild	0.596	*Gorilla gorilla*	43.71	87.39	168.90	48.25	1.92	Not Weaned

	6845			*gorilla*						
Zurich	ZURICH 6846	wild	0.625	*Gorilla gorilla gorilla*	42.21	87.76	163.99	49.25	3.74	Not Weaned
Zurich	ZURICH 6994	wild	0.635	*Gorilla gorilla gorilla*	40.10	87.46	155.72	47.75	2.44	Not Weaned
Zurich	ZURICH 7205	wild	0.601	*Gorilla gorilla gorilla*	42.20	87.89	160.17	57.63	0.00	Not Weaned
Zurich	ZURICH 7408	wild	0.591	*Gorilla gorilla gorilla*	40.01	87.13	156.43	49.38	1.72	Not Weaned
Zurich	ZURICH 7660	wild	0.538	*Gorilla gorilla gorilla*	44.64	87.88	171.06	59.25	0.00	Not Weaned
Zurich	ZURICH AS 4	wild	0.538	*Gorilla gorilla gorilla*	45.28	88.14	168.83	63.88	0.00	Not Weaned
Zurich	ZURICH 7611	wild	0.553	*Gorilla gorilla gorilla*	45.44	87.98	172.95	56.88	0.00	Not Weaned
PC	PC M22	wild	0.846	*Gorilla gorilla gorilla*	28.02	85.32	130.29	51.50	38.68	Weaned
PC	PC M691	wild	0.784	*Gorilla gorilla gorilla*	33.45	86.35	145.84	53.13	14.71	Weaned
PC	PC M868	wild	0.635	*Gorilla gorilla gorilla*	32.52	86.26	143.80	52.38	12.98	Not Weaned
PC	PC M880	wild	0.596	*Gorilla gorilla gorilla*	40.31	86.85	155.55	60.50	0.00	Not Weaned
PC	PC M98	wild	0.606	*Gorilla gorilla gorilla*	40.10	87.38	163.13	52.88	3.17	Not Weaned

PC	PC M99	wild	0.596	*Gorilla gorilla gorilla*	42.74	87.67	173.57	52.25	2.24	Not Weaned
AMNH	AMNH 167331	wild	0.596	*Gorilla gorilla gorilla*	41.93	87.36	170.86	51.25	0.22	Not Weaned
USNM	USNM 588746	wild	0.832	*Gorilla gorilla gorilla*	40.76	87.82	175.80	68.38	7.96	Weaned
RMCA	RMCA 10151	wild	0.635	*Gorilla gorilla gorilla*	43.51	87.62	166.70	58.63	0.76	Not Weaned
RMCA	RMCA 12283	wild	0.596	*Gorilla gorilla gorilla*	43.24	87.64	167.91	53.88	1.05	Not Weaned
RMCA	RMCA 75-56-M-15	wild	0.822	*Gorilla gorilla gorilla*	27.62	83.65	154.47	40.13	51.42	Weaned
RMCA	RMCA 75-56-M-20	wild	0.625	*Gorilla gorilla gorilla*	38.84	87.61	153.97	51.88	1.14	Not Weaned
RMCA	RMCA 75-56-M-19	wild	0.644	*Gorilla gorilla gorilla*	34.90	86.74	145.47	52.38	3.89	Not Weaned
RMCA	RMCA 1433	wild	0.601	*Gorilla gorilla gorilla*	45.21	87.19	165.01	55.75	1.15	Not Weaned
MCZ	MCZ 49006	wild	0.736	*Gorilla gorilla gorilla*	33.49	86.02	145.38	59.88	21.91	Not Weaned
CMNH	HTB 3402	wild	0.740	*Gorilla gorilla gorilla*	30.97	85.89	140.00	62.63	26.91	Not Weaned
CMNH	HTB 2752	wild	0.678	*Gorilla gorilla gorilla*	40.02	86.94	156.95	50.75	6.67	Not Weaned
CMNH	HTB 1921	wild	0.856	*Gorilla gorilla*	31.33	86.63	141.01	68.63	24.18	Weaned

				gorilla						
CMNH	HTB 1858	wild	0.596	*Gorilla gorilla gorilla*	46.78	87.83	179.02	50.38	1.12	Not Weaned
CMNH	HTB-1933	wild	0.635	*Gorilla gorilla gorilla*	38.04	86.68	151.51	66.00	4.23	Not Weaned
AMNH	AMNH 54328	wild	0.577	*Gorilla gorilla gorilla*	45.53	87.72	177.36	55.00	0.00	Not Weaned
PC	PC Cam 224	wild	0.567	*Gorilla gorilla gorilla*	41.12	87.52	162.93	56.63	1.49	Not Weaned
PC	PC Cam I 11	wild	0.808	*Gorilla gorilla gorilla*	37.71	86.95	157.60	63.13	8.62	Not Weaned
PC	PC M141	wild	0.596	*Gorilla gorilla gorilla*	42.67	87.20	166.76	51.63	0.44	Not Weaned
PC	PC M34	wild	0.654	*Gorilla gorilla gorilla*	40.80	87.21	156.02	60.50	8.10	Not Weaned
PC	PC M625	wild	0.625	*Gorilla gorilla gorilla*	37.91	87.23	154.78	56.63	8.75	Not Weaned
PC	PC M532	wild	0.577	*Gorilla gorilla gorilla*	43.37	87.74	167.82	52.13	0.13	Not Weaned
PC	PC M690	wild	0.577	*Gorilla gorilla gorilla*	44.07	87.20	174.37	51.75	2.50	Not Weaned
PC	PC M828	wild	0.625	*Gorilla gorilla gorilla*	45.31	87.80	171.13	50.25	3.59	Not Weaned
Zurich	ZURICH 6609	wild	0.606	*Gorilla gorilla gorilla*	38.45	87.06	162.25	55.00	0.40	Not Weaned

Zurich	ZURICH 6611	wild	0.577	*Gorilla gorilla gorilla*	41.54	87.41	161.29	53.50	0.47	Not Weaned
Zurich	ZURICH 6858	wild	0.688	*Gorilla gorilla gorilla*	29.57	84.81	137.19	60.50	12.09	Not Weaned
Zurich	ZURICH 7123	wild	0.587	*Gorilla gorilla gorilla*	48.75	87.65	176.91	55.50	0.00	Not Weaned
Zurich	ZURICH 7328	wild	0.606	*Gorilla gorilla gorilla*	40.50	87.38	164.54	54.00	0.00	Not Weaned
KBIN	KBIN 869C	wild	0.615	*Gorilla gorilla gorilla*	46.62	87.40	167.09	49.00	0.52	Not Weaned
AMNH	AMNH 86855	wild	0.563	*Pan paniscus*	42.23	88.20	162.60	52.75	0.03	Not Weaned
KBINS	KBIN 39870	wild	0.635	*Pan paniscus*	28.76	85.20	132.27	55.28	16.78	Weaned
KBINS	KBIN 874	wild	0.577	*Pan paniscus*	35.97	88.19	150.15	59.50	4.66	Not Weaned
RMCA	RMCA 29007	wild	0.553	*Pan paniscus*	44.55	88.26	167.29	53.63	0.17	Not Weaned
RMCA	RMCA 88041M	wild	0.577	*Pan paniscus*	37.53	88.02	149.65	48.00	0.25	Not Weaned
RMCA	RMCA 10198	wild	0.611	*Pan paniscus*	32.43	87.43	141.41	58.38	6.86	Weaned
RMCA	RMCA 23464	wild	0.596	*Pan paniscus*	32.79	87.00	144.87	57.25	45.74	Not Weaned
RMCA	RMCA 29003	wild	0.519	*Pan paniscus*	47.02	88.62	172.76	63.00	0.00	Not Weaned

RMCA	RMCA 29010	wild	0.625	*Pan paniscus*	43.05	88.28	165.44	51.88	1.87	Weaned
RMCA	RMCA 29013	wild	0.601	*Pan paniscus*	39.64	88.33	153.07	63.88	3.49	Not Weaned
RMCA	RMCA 29021	wild	0.635	*Pan paniscus*	36.25	87.04	154.87	57.88	30.60	Weaned
RMCA	RMCA 29024	wild	0.625	*Pan paniscus*	38.00	88.27	153.37	60.63	6.84	Not Weaned
RMCA	RMCA 29028	wild	0.731	*Pan paniscus*	30.57	87.18	147.29	50.75	29.28	Weaned
RMCA	RMCA 29030	wild	0.793	*Pan paniscus*	33.06	87.10	143.17	64.00	18.42	Weaned
RMCA	RMCA 29048	wild	0.673	*Pan paniscus*	30.53	86.14	145.17	46.00	34.70	Weaned
RMCA	RMCA 29049	wild	0.654	*Pan paniscus*	32.79	87.81	147.48	52.00	44.52	Weaned
RMCA	RMCA 29056	wild	0.731	*Pan paniscus*	22.72	84.33	123.97	47.13	42.12	Weaned
RMCA	RMCA 29058	wild	0.731	*Pan paniscus*	29.91	86.99	135.25	48.50	6.08	Weaned
RMCA	RMCA 84036M5	wild	0.668	*Pan paniscus*	40.30	88.12	160.62	55.63	1.41	Not Weaned
RMCA	RMCA 88041M	wild	0.567	*Pan paniscus*	41.88	88.24	158.64	68.00	0.86	Not Weaned
USNM	USNM	wild	0.615	*Pan paniscus*	40.08	87.72	162.50	57.00	3.45	Weaned

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Zurich	ZURICH 8502	wild	0.606	*Pan paniscus*	32.35	86.50	152.43	59.63	NA	Not Weaned
RMCA	RMCA 84036M	wild	0.524	*Pan paniscus*	42.00	88.63	162.20	50.38	0.24	Not Weaned
RMCA	RMCA 88041M	wild	0.639	*Pan paniscus*	42.93	87.96	165.36	50.63	41.84	Weaned
RMCA	RMCA 22336	wild	0.567	*Pan paniscus*	40.71	88.23	164.42	57.63	2.60	Not Weaned
RMCA	RMCA 29011	wild	0.606	*Pan paniscus*	41.31	88.10	157.96	56.50	0.00	Not Weaned
RMCA	RMCA 29019	wild	0.615	*Pan paniscus*	42.56	88.12	166.68	53.63	1.17	Weaned
RMCA	RMCA 29061	wild	0.577	*Pan paniscus*	45.16	87.97	170.92	60.13	0.20	Not Weaned
RMCA	RMCA 29043	wild	NA	*Pan paniscus*	41.05	88.04	158.81	43.50	2.72	Weaned
RMCA	RMCA 88041M	wild	0.615	*Pan paniscus*	34.44	87.24	145.55	54.00	5.49	Weaned
KBINS	KBIN 877	wild	0.587	*Pan troglodytes schweinfurthii*	37.47	87.60	146.19	60.38	0.00	Not Weaned
RMCA	RMCA 86300	wild	0.697	*Pan troglodytes schweinfurthii*	37.96	87.21	150.68	54.00	24.13	Not Weaned
RMCA	RMCA 9584	wild	0.591	*Pan troglodytes schweinfurthii*	35.15	87.62	143.19	51.63	0.00	Not Weaned

Zurich	ZURICH 6508	wild	0.625	*Pan troglodytes schweinfurthii*	40.91	87.99	151.63	51.00	1.28	Not Weaned
Zurich	ZURICH 6695	wild	0.659	*Pan troglodytes schweinfurthii*	31.70	87.34	141.25	50.00	17.39	Not Weaned
Zurich	ZURICH 7042	wild	0.587	*Pan troglodytes schweinfurthii*	42.58	87.83	162.96	50.25	0.68	Not Weaned
Zurich	ZURICH 7396	wild	0.692	*Pan troglodytes schweinfurthii*	23.40	84.23	135.30	46.25	42.37	Not Weaned
Zurich	ZURICH 7659	wild	0.558	*Pan troglodytes schweinfurthii*	43.90	88.11	164.38	50.75	0.00	Not Weaned
RMCA	RMCA 20481	wild	0.577	*Pan troglodytes schweinfurthii*	43.62	87.30	161.16	49.63	0.00	Not Weaned
RMCA	RMCA 29093	wild	0.654	*Pan troglodytes schweinfurthii*	28.64	86.63	134.06	44.63	42.68	Not Weaned
AMNH	AMNH 51405	wild	0.558	*Pan troglodytes schweinfurthii*	44.40	88.27	169.45	65.75	0.00	Not Weaned
AMNH	AMNH 51206	wild	0.538	*Pan troglodytes schweinfurthii*	39.94	88.17	161.36	52.38	0.35	Not Weaned
AMNH	AMNH 51211	wild	0.764	*Pan troglodytes schweinfurthii*	34.14	87.38	141.77	58.38	6.59	Weaned
AMNH	AMNH 51391	wild	0.644	*Pan troglodytes schweinfurthii*	40.87	88.09	151.40	58.75	0.72	Not Weaned
KBIN	KBIN 7111	wild	0.567	*Pan troglodytes schweinfurthii*	38.37	88.06	148.31	50.25	0.00	Not Weaned
RMCA	RMCA 559	wild	0.712	*Pan troglodytes*	28.10	86.21	133.65	46.75	46.95	Weaned

				schweinfurthii						
RMCA	RMCA 25491	wild	0.606	*Pan troglodytes schweinfurthii*	35.36	87.91	144.12	62.25	0.74	Not Weaned
RMCA	RMCA 5894	wild	0.654	*Pan troglodytes schweinfurthii*	30.70	86.99	132.11	61.13	2.96	Not Weaned
RMCA	RMCA 13718	wild	0.567	*Pan troglodytes schweinfurthii*	40.65	88.26	150.06	58.25	0.26	Not Weaned
RMCA	RMCA 6035	wild	0.654	*Pan troglodytes schweinfurthii*	31.45	87.43	133.61	43.38	0.00	Not Weaned
RMCA	RMCA 91060M	wild	0.793	*Pan troglodytes schweinfurthii*	31.66	87.22	139.82	56.00	10.83	Weaned
RMCA	RMCA 302	wild	0.577	*Pan troglodytes schweinfurthii*	36.53	87.65	140.81	52.00	0.83	Not Weaned
RMCA	RMCA 10415	wild	0.582	*Pan troglodytes schweinfurthii*	37.89	87.54	150.75	54.75	0.98	Not Weaned
RMCA	RMCA 10734	wild	0.538	*Pan troglodytes schweinfurthii*	42.22	88.16	161.92	55.50	0.06	Not Weaned
RMCA	RMCA 10735	wild	0.611	*Pan troglodytes schweinfurthii*	38.02	88.12	150.56	53.25	2.96	Not Weaned
RMCA	RMCA 10736	wild	0.635	*Pan troglodytes schweinfurthii*	28.30	86.54	134.59	49.50	47.26	Not Weaned
RMCA	RMCA 11157	wild	0.591	*Pan troglodytes schweinfurthii*	40.16	87.77	158.58	53.88	0.26	Not Weaned
RMCA	RMCA 129454	wild	0.538	*Pan troglodytes schweinfurthii*	37.95	88.11	141.70	48.00	0.00	Not Weaned

RMCA	RMCA 13759	wild	0.615	*Pan troglodytes schweinfurthii*	39.25	88.19	151.67	53.63	0.23	Not Weaned
RMCA	RMCA 690	wild	0.625	*Pan troglodytes schweinfurthii*	34.76	87.44	141.21	51.88	0.12	Not Weaned
USNM	USNM 23672	wild	0.635	*Pan troglodytes schweinfurthii*	37.08	87.83	150.81	55.25	0.42	Not Weaned
AMNH	AMNH 51388	wild	0.663	*Pan troglodytes schweinfurthii*	36.54	87.79	148.94	56.38	1.64	Not Weaned
RMCA	RMCA 12954	wild	0.538	*Pan troglodytes schweinfurthii*	37.96	88.11	141.69	47.75	0.20	Not Weaned
RMCA	RMCA 6971	wild	0.673	*Pan troglodytes schweinfurthii*	28.62	86.25	136.18	65.88	10.08	Not Weaned
KBINS	KBIN 34928	wild	0.625	*Pan troglodytes schweinfurthii*	38.33	88.02	151.24	51.63	0.77	Not Weaned
RMCA	RMCA 29068	wild	0.567	*Pan troglodytes schweinfurthii*	41.11	88.24	160.46	47.88	1.46	Not Weaned
RMCA	RMCA 29070	wild	0.567	*Pan troglodytes schweinfurthii*	37.45	87.89	151.74	48.38	9.96	Not Weaned
KBIN	KBIN 39901	wild	0.625	*Pan troglodytes schweinfurthii*	39.37	87.70	151.11	52.75	0.60	Not Weaned
RMCA	RMCA 5570	wild	0.625	*Pan troglodytes schweinfurthii*	35.06	87.82	149.53	59.63	1.33	Not Weaned
RMCA	RMCA 29072	wild	0.760	*Pan troglodytes schweinfurthii*	37.05	87.83	150.54	58.63	0.92	Not Weaned
RMCA	RMCA	wild	0.654	*Pan troglodytes*	37.92	88.10	149.98	55.38	0.37	Not Weaned

	29076			*schweinfurthii*						
RMCA	RMCA 28711	wild	0.707	*Pan troglodytes schweinfurthii*	27.57	86.30	135.30	53.50	54.71	Weaned
RMCA	RMCA 4190	wild	0.567	*Pan troglodytes schweinfurthii*	41.43	88.39	156.74	54.13	0.00	Not Weaned
MCZ	MCZ 19188	wild	0.793	*Pan troglodytes troglodytes*	26.11	83.43	131.31	54.50	36.27	Not Coded
MCZ	MCZ 26848	wild	0.692	*Pan troglodytes troglodytes*	34.06	86.99	147.15	66.75	9.07	Not Coded
MCZ	MCZ 34101	wild	0.625	*Pan troglodytes troglodytes*	36.87	87.64	145.53	55.00	6.03	Not Coded
MCZ	MCZ 42129	wild	0.668	*Pan troglodytes troglodytes*	25.47	86.63	125.76	50.88	5.77	Not Coded
MCZ	MCZ 42154	wild	0.745	*Pan troglodytes troglodytes*	26.58	85.87	127.83	40.63	22.38	Not Coded
MCZ	MCZ 9495	wild	0.591	*Pan troglodytes troglodytes*	34.58	87.72	139.65	48.50	5.03	Not Coded
PC	PC M03	wild	0.625	*Pan troglodytes troglodytes*	33.08	87.27	145.17	50.88	9.18	Not Coded
PC	PC M133	wild	0.625	*Pan troglodytes troglodytes*	33.40	86.60	141.29	45.13	1.77	Not Coded
PC	PC M173	wild	0.582	*Pan troglodytes troglodytes*	41.71	87.87	155.06	45.75	0.07	Not Coded
PC	PC M182	wild	0.654	*Pan troglodytes troglodytes*	36.98	87.94	153.46	48.88	4.46	Not Coded

PC	PC M250	wild	0.620	*Pan troglodytes troglodytes*	34.74	87.25	141.41	53.38	4.39	Not Coded
PC	PC M300	wild	0.625	*Pan troglodytes troglodytes*	33.01	87.06	140.06	49.25	2.66	Not Coded
PC	PC M358	wild	0.678	*Pan troglodytes troglodytes*	37.27	88.22	146.92	58.00	39.04	Not Coded
PC	PC M363	wild	0.721	*Pan troglodytes troglodytes*	31.95	86.88	142.00	50.25	4.59	Not Coded
PC	PC M369	wild	0.649	*Pan troglodytes troglodytes*	31.35	87.57	136.36	49.25	23.13	Not Coded
PC	PC M397	wild	0.635	*Pan troglodytes troglodytes*	34.56	87.94	140.47	48.88	4.11	Not Coded
PC	PC M451	wild	0.654	*Pan troglodytes troglodytes*	30.61	87.42	134.29	53.00	5.80	Not Coded
PC	PC M453	wild	0.716	*Pan troglodytes troglodytes*	32.50	87.03	138.16	42.25	4.46	Not Coded
PC	PC M454	wild	0.832	*Pan troglodytes troglodytes*	25.61	86.14	129.64	53.38	25.35	Not Coded
PC	PC M475M	wild	0.567	*Pan troglodytes troglodytes*	40.91	87.96	148.93	48.25	0.00	Not Coded
PC	PC M507	wild	0.721	*Pan troglodytes troglodytes*	31.15	86.66	135.36	41.63	6.19	Not Coded
PC	PC M60	wild	0.673	*Pan troglodytes troglodytes*	35.68	87.44	142.60	51.88	3.96	Not Coded
PC	PC M675	wild	0.712	*Pan troglodytes*	34.29	87.85	140.14	59.88	16.48	Not Coded

				troglodytes						
PC	PC M746	wild	0.784	*Pan troglodytes troglodytes*	29.14	85.81	135.12	54.38	42.43	Not Coded
PC	PC M754	wild	0.659	*Pan troglodytes troglodytes*	36.31	88.11	148.72	52.00	27.57	Not Coded
PC	PC M777	wild	0.596	*Pan troglodytes troglodytes*	39.52	87.96	152.42	44.50	2.11	Not Coded
PC	PC M876	wild	0.663	*Pan troglodytes troglodytes*	31.45	87.24	136.06	56.38	1.64	Not Coded
PC	PC M891	wild	0.808	*Pan troglodytes troglodytes*	25.71	86.03	125.46	50.63	35.36	Not Coded
PC	PC M94	wild	0.745	*Pan troglodytes troglodytes*	32.54	86.93	143.11	51.25	44.82	Not Coded
PC	PC Mer II 2	wild	0.683	*Pan troglodytes troglodytes*	25.48	85.83	127.73	74.25	23.30	Not Coded
Zurich	ZURICH 6613	wild	0.644	*Pan troglodytes troglodytes*	30.88	87.54	134.91	52.38	5.21	Not Coded
USNM	USNM 174708	wild	0.654	*Pan troglodytes troglodytes*	35.41	87.34	146.03	58.75	1.24	Not Coded
USNM	USNM 176233	wild	0.678	*Pan troglodytes troglodytes*	34.59	87.43	143.45	59.25	6.64	Not Coded
USNM	USNM 236972	wild	0.635	*Pan troglodytes troglodytes*	37.10	87.83	150.91	54.25	0.63	Not Coded
CMNH	HTB 1881	wild	0.635	*Pan troglodytes troglodytes*	31.87	86.88	143.06	51.63	11.08	Not Coded

CMNH	HTB 1848	wild	0.538	*Pan troglodytes troglodytes*	41.31	87.86	152.70	53.50	0.00	Not Coded
CMNH	HTB 1176	wild	0.577	*Pan troglodytes troglodytes*	37.70	87.92	148.84	53.25	0.51	Not Coded
MCZ	MCZ 19189	wild	0.793	*Pan troglodytes troglodytes*	28.28	86.26	133.42	72.38	11.89	Not Coded
MCZ	MCZ 23166	wild	0.683	*Pan troglodytes troglodytes*	40.75	87.86	155.40	55.63	26.61	Not Coded
PC	PC M152 3rd	wild	0.553	*Pan troglodytes troglodytes*	43.20	87.98	166.11	51.88	0.38	Not Coded
PC	PC M145 3rd	wild	0.760	*Pan troglodytes troglodytes*	27.37	86.01	131.93	55.88	26.73	Not Coded
PC	PC M911	wild	0.663	*Pan troglodytes troglodytes*	33.03	87.12	140.11	50.25	10.52	Not Coded
PC	PC M556	wild	0.577	*Pan troglodytes troglodytes*	38.54	87.98	151.77	53.00	3.25	Not Coded
PC	PC M635	wild	0.750	*Pan troglodytes troglodytes*	29.98	86.66	135.84	58.13	14.21	Not Coded
PC	PC M930	wild	0.644	*Pan troglodytes troglodytes*	31.90	87.58	137.90	49.00	8.28	Not Coded
PC	PC M781	wild	0.543	*Pan troglodytes troglodytes*	41.28	88.42	160.73	60.63	0.85	Not Coded
PC	PC M888	wild	0.538	*Pan troglodytes troglodytes*	43.18	88.03	159.76	55.00	0.27	Not Coded
Zurich	ZURICH	wild	0.538	*Pan troglodytes*	38.07	88.37	154.31	62.50	0.60	Not Coded

	6675			*troglodytes*						
PC	PC 665	wild	0.635	*Pan troglodytes troglodytes*	34.14	87.76	143.64	51.38	2.21	Not Coded
Zurich	ZURICH 6615	wild	0.625	*Pan troglodytes troglodytes*	35.38	87.11	146.61	50.63	24.73	Not Coded
Zurich	ZURICH 6531	wild	0.630	*Pan troglodytes troglodytes*	40.53	87.47	154.96	55.38	1.56	Not Coded
USNM	USNM 220067	wild	0.639	*Pan troglodytes troglodytes*	36.10	87.85	144.77	57.63	1.02	Not Coded
USNM	USNM 176234	wild	0.736	*Pan troglodytes troglodytes*	36.55	87.48	151.39	54.00	8.61	Not Coded
MCZ	MCZ 50959	wild	0.712	*Pongo abelii*	30.81	86.95	135.94	48.25	2.74	Not Coded
Zurich	ZURICH 1014	captive	0.654	*Pongo abelii*	27.82	86.41	131.56	51.00	6.72	Not Coded
ZSM	ZSM 1910 122	wild	0.625	*Pongo abelii*	32.33	86.99	143.68	51.88	0.84	Not Coded
Zurich	ZURICH AS 1566	wild	0.606	*Pongo abelii*	33.60	87.54	143.15	59.13	1.23	Not Coded
USNM	USNM 143595	wild	0.615	*Pongo abelii*	32.21	87.42	135.15	55.63	1.60	Not Coded
USNM	USNM 143599	wild	0.615	*Pongo abelii*	34.03	87.26	140.34	53.88	0.54	Not Coded
ZSM	ZSM 1981 246	wild	0.615	*Pongo abelii*	31.20	87.18	139.30	55.63	0.83	Not Coded

USNM	USNM 143586	wild	0.654	*Pongo abelii*	34.28	86.98	148.05	57.38	3.59	Not Coded
CNHM	HTB 1024	wild	0.702	*Pongo abelii*	34.94	87.77	143.70	54.00	2.25	Not Coded
AMNH	AMNH 150227	wild	0.615	*Pongo pygmaeus*	36.31	87.98	145.02	60.88	0.31	Not Weaned
AMNH	AMNH 200899	wild	0.596	*Pongo pygmaeus*	38.44	88.04	147.87	62.25	0.29	Not Weaned
AMNH	AMNH 77798	wild	0.587	*Pongo pygmaeus*	33.97	86.89	139.80	50.25	0.44	Not Weaned
MCZ	MCZ 5059	wild	0.538	*Pongo pygmaeus*	36.74	87.84	143.39	59.63	0.00	Not Weaned
MCZ	MCZ 5290	wild	0.615	*Pongo pygmaeus*	34.72	87.92	140.37	54.50	5.60	Not Weaned
MCZ	MCZ 413	wild	0.692	*Pongo pygmaeus*	31.73	87.25	137.28	48.25	4.19	Not Weaned
ZSM	ZSM 1907 312	wild	0.635	*Pongo pygmaeus*	36.53	88.14	143.08	67.50	0.13	Not Weaned
ZSM	ZSM 1907 0483	wild	0.577	*Pongo pygmaeus*	38.70	88.32	148.16	71.25	0.00	Not Weaned
ZSM	ZSM 1907 0380	wild	0.793	*Pongo pygmaeus*	30.67	86.52	135.37	57.13	17.31	Not Weaned
ZSM	ZSM 1907 0643	wild	0.606	*Pongo pygmaeus*	38.63	88.25	149.30	68.50	0.58	Not Weaned
ZSM	ZSM 1981 137	wild	0.577	*Pongo pygmaeus*	36.80	88.28	143.47	61.13	0.57	Not Weaned

ZSM	ZSM 1981 72	wild	0.567	*Pongo pygmaeus*	38.99	87.97	151.52	64.00	0.00	Not Weaned
ZSM	ZSM 1981 55	wild	0.481	*Pongo pygmaeus*	40.10	87.92	168.76	58.88	0.00	Not Weaned
ZSM	ZSM 1981 131	wild	0.577	*Pongo pygmaeus*	39.11	88.13	150.17	54.88	0.46	Not Weaned
ZSM	ZSM1981 210	wild	0.692	*Pongo pygmaeus*	34.16	87.05	142.05	53.75	2.12	Not Weaned
ZSM	ZSM 1981 21	wild	0.678	*Pongo pygmaeus*	38.76	87.72	149.13	54.38	NA	Not Weaned
ZSM	ZSM 1981 221	wild	0.779	*Pongo pygmaeus*	32.37	86.52	145.00	49.75	20.14	Weaned
ZSM	ZSM1981 98	wild	0.567	*Pongo pygmaeus*	36.58	88.12	143.95	60.25	0.00	Not Weaned
ZSM	ZSM 1981 115	wild	0.683	*Pongo pygmaeus*	35.53	87.70	148.06	56.75	1.17	Not Weaned
ZSM	ZSM 1981 236	captive	0.548	*Pongo pygmaeus*	35.87	87.97	138.66	62.13	0.00	Not Weaned
ZSM	ZSM1981 43	wild	0.726	*Pongo pygmaeus*	28.06	86.89	127.53	54.63	5.34	Weaned
ZSM	ZSM 1981 48	wild	0.702	*Pongo pygmaeus*	30.33	86.38	135.04	50.38	6.84	Weaned
ZSM	ZSM 1981 57	wild	0.577	*Pongo pygmaeus*	33.14	87.36	137.70	54.50	0.69	Not Weaned
ZSM	ZSM 1981	wild	0.577	*Pongo*	36.94	87.44	144.62	58.88	2.22	Not Weaned

	65			*pygmaeus*						
ZSM	ZSM 1981 127	wild	0.784	*Pongo pygmaeus*	33.94	87.31	147.58	60.63	11.76	Weaned
Zurich	Zurich AS 1471	wild	0.668	*Pongo pygmaeus*	34.24	87.52	141.42	48.88	2.25	Not Weaned
Zurich	Zurich AS 1767	wild	0.731	*Pongo pygmaeus*	32.63	87.04	139.64	53.88	3.30	Weaned
ZSM	ZSM 1981 52	wild	0.625	*Pongo pygmaeus*	34.43	88.04	140.20	70.13	0.28	Not Weaned
CNHM	HTB 1440	wild	0.760	*Pongo pygmaeus*	35.10	88.08	141.71	57.38	1.05	Not Weaned
ZSM	ZSM 1981 224	wild	0.808	*Pongo pygmaeus*	29.94	85.35	135.08	47.75	13.01	Weaned
Zurich	Zurich AS 1540	wild	0.615	*Pongo pygmaeus*	36.31	87.96	149.51	56.13	0.11	Not Weaned
USNM	USNM 142171	wild	0.620	*Pongo pygmaeus*	32.60	87.66	136.01	66.63	0.09	Not Weaned
USNM	USNM 153821	wild	0.861	*Pongo pygmaeus*	32.82	87.31	142.13	64.88	10.95	Weaned
USNM	USNM 292562	captive	0.587	*Pongo pygmaeus*	37.19	88.34	143.88	52.88	0.00	Not Weaned
USNM	USNM 317197	wild	0.529	*Pongo pygmaeus*	39.44	88.27	151.72	60.25	0.00	Not Weaned
USNM	USNM 396920	wild	0.548	*Pongo pygmaeus*	42.64	88.12	158.25	69.25	0.02	Not Weaned

Zurich	Zurich AS 1646	wild	0.620	*Pongo pygmaeus*	29.06	85.73	137.86	47.13	5.99	Not Weaned
KBINS	KBINS 861 F	wild	0.500	*Pongo pygmaeus*	39.89	88.62	152.88	75.38	0.00	Not Weaned
KBINS	KBINS 863 D	wild	0.558	*Pongo pygmaeus*	38.14	87.89	152.25	63.13	0.43	Not Weaned
ZSM	ZSM 1981 37	wild	0.721	*Pongo pygmaeus*	31.29	86.85	137.64	60.25	12.35	Weaned
ZSM	ZSM 1981 42	wild	0.745	*Pongo pygmaeus*	34.23	87.40	142.64	58.25	1.69	Not Weaned

APPENDIX B

PYTHON SCRIPTS FOR DATA COLLECTION IN GRASS GIS

Script Objective: Scan ASCII file for extents then generate DEM via the mean

```
#!/usr/bin/env python
#%Module
#% description: Scan ASCII file for extents then generate
DEM via the mean
#%End
#%option
#% key: textfile
#% gisprompt: file,file,file
#% description: Enter xyz ascii file
#% required: yes
#%end
#%option
#% key: dem
#% type: string
#% gisprompt: out, cell, raster
#% description: Name for output map
#% required: yes
#%end
#%option
#% key: scanres
#% type: double
#% description: Scan resolution
#% required: yes
#% answer: 0.05
#%end
#% flag
#% key: o
#% description: Allow output files to overwrite existing
files
#%end

import sys
from grass.script import core as grass

def main():
    textfile = options['textfile']
    dem = options['dem']
    scanres = float(options['scanres'])
    setregion(textfile,dem,scanres)

def setregion(textfile,dem, scanres):
```

```
    p = grass.pipe_command("r.in.xyz",overwrite=True,
flags="g",input = textfile, output = dem,separator =',')
    extents = p.communicate()[0]
    print "extents = ",extents
    offset = scanres/2
    print "offset2 =", offset
    paramlist = extents.split()
    print 'paramlist =',paramlist
    next = float(paramlist[0].split('=')[1]) + offset
    sext = float(paramlist[1].split('=')[1]) - offset
    eext = float(paramlist[2].split('=')[1]) + offset
    wext = float(paramlist[3].split('=')[1]) - offset
    bext = float(paramlist[4].split('=')[1]) - offset
    text = float(paramlist[5].split('=')[1]) - offset

    grass.run_command('g.region',n=next, s=sext, e=eext,
w=wext, b=bext, t=text, res=scanres)
    region = grass.region()
    print 'region', region
    grass.run_command('r.in.xyz', overwrite=True, input =
textfile, output = dem, separator =',')

if __name__ == "__main__":
    options, flags = grass.parser()
    main()
```

Script Objective: To automate generating slopes and angularity data and then save them to get stats

```
#!/usr/bin/env python
############################################################
########################################
#
# Module:       catlett_slope.py
# Author:       Kierstin Catlett
# Purpose:      To automate generating slopes and
angularity and saving them as slopes to get stats
############################################################
########################################

#Following code is run GRASS commands without starting
GRASS GUI
import sys
import os
```

```
import grass.script as grass
import grass.script.setup as gsetup
gisbase = os.environ['GISBASE']
gisdb="/Users/kierstincatlett/GrassData"
location="Dissertation_Data_2013"
mapset="methods_check"
gsetup.init(gisbase, gisdb, location, mapset)
from grass.script import core as g
import csv
import itertools

#First try on an individual file

teeth = grass.parse_command("g.list", _type="rast")
#print teeth
teeth2 = dict.keys(teeth)[1].split( )
#print teeth2

for items in teeth2:
    dem=items
    slope= items + "_slope"
    print dem
    setregion = grass.run_command('g.region', rast=dem,
flags='pg', zoom=dem, align=dem)
    print setregion
    getslope = grass.run_command('r.slope.aspect',
elevation=dem, slope=slope)
    print getslope

teeth3 = grass.parse_command("g.list", _type="rast")
#print teeth3
teeth4 = dict.keys(teeth)[2].split( )
print teeth4

for items4 in teeth4:
    dem4=items4
    print dem4
    slope= items4 + "_ang"
    setregion = grass.run_command('g.region', rast=dem4,
flags='pg', zoom=dem4, align=dem4)
    print setregion
    getslope = grass.run_command('r.slope.aspect',
elevation=dem4, slope=slope)
    print getslope
```

```
#teeth5 = grass.parse_command("g.list", _type="rast")
#print teeth5


#def main():
#    teeth = grass.parse_command("g.list", _type="rast")
#    print teeth
#    print len(teeth)
#    print type(teeth)
#    teeth2 = dict.keys(teeth)[1].split( )
#    print teeth2
#    #print type(teeth2) #teeth2 is a list
#    for items in teeth2:
#        getregion = grass.run_command('g.region',
rast=items, flags='pg', zoom=items, align=items)
#        print getregion
#                output = items + str(slope)
#                getslope =
grass.run_command('r.slope.aspect', elevation=items,
slope=output)
#                print getslope

#if __name__ == "__main__":
#    options, flags = grass.parser()
#    main()
```

Script Objective: Convert raster map to vector map then back to raster map to collect 3D and 2D area for relief index data and 2D area for dentine exposure data.

```
#!/usr/bin/env python
############################################################
####################
#
# Module:       kayv7.py
# Author:       Kierstin Catlett for Dissertation (modified
April 2, 2012)
# Purpose:      Convert raster to vector to raster to
collect 3D and 2D area
############################################################
####################
#%Module
#% description: Collect 2D and 3D area
```

```
#%End
#%option
#% key: input
#% type: string
#% gisprompt: old,cell,raster
#% key_desc: name
#% description: Name of input raster map
#% required: yes
#%end
#%option
#% key: output
#% type: string
#% gisprompt: new_file, file, output
#% key_desc: name
#% description: Name for output vector file (if omitted or
"-" output to stdout)
#% required: yes
#%end
#%option
#% key: output2
#% type: string
#% gisprompt: new,cell,raster
#% key_desc: name
#% description: Name of output raster map for 2D area
#% required: yes
#%end
#%option
#% key: use
#% type: string
#% description: Source of raster values
#% answer: val
#%end
#%option
#% key: feature
#% type: string
#% description: Feature type (point)
#% required: yes
#% answer: point
#%end
#%option
#%end
#% flag
#% key: o
#% description: Allow output files to overwrite existing
files
#%end
```

```
import sys
import os
import string
import grass.script as grass
#from grass.script import core as grass

def main():
   input = options['input']
   output = options['output']
   output2 = options ['output2']
   setregion(input)

# Set region to match this raster
# Shrink region until it meets non-NULL data from this
raster map
# Convert raster to vector then back to raster based on val
to get 2D area
# Print original raster file name
# Print 3D and 2D area
def setregion(input):
    p = grass.pipe_command('g.region',rast =
options['input'], zoom = options['input'])
    region = grass.region()
    grass.run_command('r.to.vect', type = 'point', input =
options['input'], output = options['output'])
    grass.run_command('v.to.rast', use = 'val', input
=options['output'], output =options['output2'])
    grass.run_command('r.surf.area', map =
options['input'])
    grass.run_command('r.surf.area', map =
options['output2'])
    print 'input', input
    print 'region', region

if __name__ == "__main__":
    options, flags = grass.parser()
    main()
```

Script Objective: Set region to easily print out univariate stats (e.g., collect data).

```
#!/usr/bin/env python
```

```
############################################################
####################
#
# Module:       kay_stats.py
# Author:       Kierstin Catlett for Dissertation
# Purpose:      Set region to easily print out univariate
stats for maps
############################################################
####################
#%Module
#% description: Sets region for each  map to print out
univariate stats
#%End
#%option
#% key: input
#% type: string
#% gisprompt: old,cell,raster
#% key_desc: name
#% description: Select input raster maps
#% required: yes
#%end
#% flag
#% key: o
#% description: Allow output files to overwrite existing
files
#%end

import sys
from grass.script import core as grass

def main():
   input = options['input']
   setregion(input)
   map = options['input']

# Set region to match this raster
# Print Univarte Stats extended stats in comma delimted
table format

def setregion(input):
    p = grass.pipe_command('g.region',rast =
options['input'], zoom = options['input'])
    region = grass.region()
    grass.run_command('r.univar', flags="t", map =
options['input'],fs=",")
    print 'input', input
```

```
    print 'region', region


if __name__ == "__main__":
    options, flags = grass.parser()
    main()
```

APPENDIX C

PYTHON SCRIPTS FOR DATA COLLECTION IN GRASS GIS

Chapter 2 R-Code

```
#Packages Required
require(ggplot2)
require(plyr)
require(knitr)
require(dunn.test)
require(segmented)
require(psych)

#Load Data Set
name.dat<-Loaded_Data_Set
#Code variables for X and Y
x<-name.dat$dental_score
y<-name.dat$slope_mean
y<-name.dat$ang_mean
y<-name.dat$RFI
y<-name.dat$OPCRs
y<-name.dat$PDE_2D
#To replicate numbers in segemented package set.seed
set.seed(50)
#Assess Data
plot(x,y)
#Calcuate linear models and segmented models
lin.mod <- lm(y~x)
summary(lin.mod)
segmented.mod <- segmented(lin.mod, seg.Z = ~x)
summary(segmented.mod)
intercept(segmented.mod)
slope(segmented.mod)
print(segmented.mod)
plot(x,y)
plot(segmented.mod, add=T)
#Create data frame to plot a segemented regression in
GGPLOT
dat2 <- data.frame(x = x, y =
broken.line(segmented.mod)$fit)
#Davies' Test test if change in the slope is significant
davies.test(lin.mod, seg.Z=~x)
#AIC code to compare the linear and segemented models
AICc_output <- AICc(lin.mod,segmented.mod)
AICc_output
Weights(AICc_output)
#Code for GGPLOT graphics for Chapater 2
#Change values as appropriate for each graph. Below are two
examples. The first one is for plotting the regression in
gglplot when the linear model was best. The second example
```

is for when the segmented regression was best. Note the key difference is use "geom_line" and to use the dat2 (the data frame created)

```
#Example if linear model was best:
ggplot(abelii.dat, aes(x = x, y=y)) + geom_point(size=4,
shape=15) + geom_smooth(method="lm", se=FALSE, color =
"blue") + labs(title="Pongo abelii", xlab ="Dental Score",
ylab="OPCR") + coord_cartesian((ylim=c(40,80,5))) +
coord_cartesian((xlim=c(0.45, 1.0, 0.50))) + ggtitle("Pongo
abelii") + labs(x="Dental Score",y="OPCR")+
theme(plot.title=element_text(size=18, face="italic"),
axis.title=element_text(size=16, face="bold"),
axis.text=element_text(size=12)) + annotate(geom="text",
x=0.85, y=100, label="y = 86.83 - 50.84x, adj. r^2=0.266",
colour="blue", size=5)

#Example if segmented model was best:
ggplot(pygmaeus.dat, aes(x = x, y=y)) + geom_point(size=4,
shape=17) + geom_line(data=dat2, color = "blue") +
labs(title="Pongo pygmaeus", xlab ="Dental Score",
ylab="RFI") + coord_cartesian((ylim=c(120,200, 10))) +
coord_cartesian((xlim=c(0.45, 1.0, 0.50))) + ggtitle("Pongo
pygmaeus") + labs(x="Dental Score",y="RFI")+
theme(plot.title=element_text(size=18, face="italic"),
axis.title=element_text(size=16, face="bold"),
axis.text=element_text(size=12)) + annotate(geom="text",
x=0.90, y=178, label="y1 =  593.9 - 883.90x", colour="blue",
size=5) + annotate(geom="text", x=0.90, y=175, label="y2 =
163.1 - 30.76x", colour="blue", size=5) +
annotate(geom="text", x=0.90, y=172, label="adj. r^2=
0.4211", colour="blue", size=5) + annotate(geom="text",
x=0.90, y=169, label="bk =  0.505", colour="blue", size=5)
+  geom_vline(aes(xintercept=0.505), colour="black",
linetype="dashed")
```

```
GLM Rslope_m Rang_mea RRFI RNoClump RPDE_2D BY
Genus_sps_sbs_pooled Binary_Wean_Range
  /CONTRAST(Genus_sps_sbs_pooled)=Simple
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /POSTHOC=Genus_sps_sbs_pooled(TUKEY LSD BONFERRONI SIDAK)
  /PLOT=PROFILE(Genus_sps_sbs_pooled*Binary_Wean_Range)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Genus_sps_sbs_pooled*Binary_Wean_Range)
  /PRINT=DESCRIPTIVE ETASQ OPOWER HOMOGENEITY
  /CRITERIA=ALPHA(.05)
  /DESIGN= Genus_sps_sbs_pooled Binary_Wean_Range
Genus_sps_sbs_pooled*Binary_Wean_Range.


DISCRIMINANT
  /GROUPS=Species_Pooled_Code(1 7)
  /VARIABLES=Rslope_m Rang_mea RRFI RNoClump RPDE_2D
  /SELECT=Binary_Wean_Range(0)
  /ANALYSIS ALL
  /SAVE=SCORES
  /PRIORS EQUAL
  /STATISTICS=MEAN STDDEV UNIVF BOXM RAW GCOV TABLE
  /PLOT=COMBINED SEPARATE  MAP
  /CLASSIFY=NONMISSING POOLED.


DISCRIMINANT
  /GROUPS=Species_Pooled_Code(1 7)
  /VARIABLES=Rslope_m Rang_mea RRFI RNoClump RPDE_2D
  /SELECT=Binary_Wean_Range(1)
  /ANALYSIS ALL
  /SAVE=SCORES
  /PRIORS EQUAL
  /STATISTICS=MEAN STDDEV UNIVF BOXM RAW GCOV TABLE
  /PLOT=COMBINED SEPARATE  MAP
  /CLASSIFY=NONMISSING POOLED.
```

Chapter 4 – R-Code

```
#Packages Required
require(plyr)
require (smatr)
require(ggplot2)

#Load Data Sets
lemur.dat <- Lemur_Data_For_2016_ICM_R
poster.dat <-Avahi_poster_data_For_R
#Subset data into species and Families
#Example:
Cheirogaleus_major.dat <-
lemur.dat[which(lemur.dat$Species=='Cheirogaleus_major'),]

#BELOW IS THE TEST OF THE IC MODEL (Evans et al., 2007)
With SMA
#Example based on the maxillary molars
x<- lemur.dat$M2M1_upper_area
y<- lemur.dat$M3M1_upper_area
upper_molars <- sma(y~x, slope.test = 2, elev.test = -1)
upper_molars
summary(upper_molars)
plot(upper_molars, xlab="M2/M1", ylab="M3/M1",
main="Maxillary Molars", pch=2, cex.main=1.5, col="blue")


#Example of calculating linear regressions for each species
aye_aye_lm <-
lm(Daubentonia_madagascariensis.dat$Lower_Area~Daubentonia_
madagascariensis.dat$Lower_Code)
summary(aye_aye_lm)

#Example of plotting the results of SMA for maxillary
molars
plot1 <- ggplot(lemur.dat, aes(x=M2M1_upper_area,
y=M3M1_upper_area, label=rownames(lemur.dat2))) +
geom_text(size=6) + ggtitle("Maxillary Molars") +
xlab("M2/M1") + ylab("M3/M1") + theme(plot.title =
element_text(color="black", size=20, face="bold"),
axis.title.x = element_text(color = "black", size=16,
face="bold"), axis.title.y=element_text(color = "black",
size=16, face="bold"), axis.text.x = element_text(colour =
"black", size=12), axis.text.y=element_text(colour =
"black", size=12))
```

```
plot1 + geom_abline(intercept = -1.2877410, slope =
1.923176) + geom_abline(intercept = -1.0, slope = 2.0,
linetype=2)
```